The influence of ice disturbance on nearshore benthic communities at Adelaide Island, Antarctica

Thesis

The influence of ice disturbance on nearshore benthic communities at Adelaide Island, Antarctica

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By

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"It's the little things that make me so happy; all I wanna do is live by the sea.
It's the little things that make me so happy; it's good, yes it's good, good to be free."

Noel Gallagher, 1994.

Abstract

Ice disturbance is frequently cited as having a major role in structuring benthic communities in shallow polar waters, and yet comprehensive field studies on the direct effects of ice disturbance are rare. This thesis aimed to describe the role of ice disturbance in determining benthic community structure at sites around Rothera Point, Adelaide Island (67° 34.5′ S, 68° 07.0′ W). The work comprised of two main components; a range of observational studies to describe the general effects of ice disturbance, and an experimental quantification of the disturbance pressure, which was then used to make novel links between disturbance and community structure.

A photographic survey using depth transects (0-35 m depth) at three sites showed that benthic assemblages changed continuously along a bathymetric gradient. Assemblages were most patchy at shallow depths and the relative abundance of sessile forms increased with depth, which suggested that disturbance intensity was greatest in the shallows. The immediate effects of iceberg impacts were also investigated. Communities within newly formed iceberg scours were sampled and compared with those in undisturbed areas; scoured assemblages were 95% lower in mean macrofaunal abundance and 75.9% lower in species richness. The recovery of three scour assemblages was monitored for ~30 months following the disturbance event. Scoured assemblages became increasingly similar to undisturbed assemblages over time and marked spatial variability was observed in both scoured and unscoured zones.

Experimental markers were designed to detect iceberg impacts and were deployed as 24 grids at four depth increments and two study sites. Markers were surveyed regularly for two years to quantify the frequency of iceberg impacts, which varied significantly with depth, site, season and year. The intensity of disturbance was greatest in the shallows (0-5 m depth) and significantly reduced at 25 m depth. Variation between site and season could be largely explained by the duration of winter fast ice. Extensive sampling at each of the disturbance grids showed that disturbance intensity has a significant and wide-ranging influence on macrobenthic community structure.

Acknowledgements

Looking back at an incredible two and a half years living and working at Rothera Research Station, I realise that Antarctica has given me a lot more than just a rare opportunity to see a beautiful part of our remarkable planet. A few of these unexpected bonuses, and the people involved, are worth a mention:

- During my time 'South' I met a number of fascinating characters, some of which I have not managed to lose along the way. Matt, Paul, John, Andy, Kirk, Ags, Tim, Rob, Hamish, Jools, Ads and Vacant, cheers for the laughs and keep 'em coming.
- As a young man fresh out of university, living in isolation with 20 other people for 16 months made me realise how interesting human beings actually are. I would like to thank all the winterers of 2004 and 2005 for making the time so memorable.
- Special thanks to Dive Officers Matt Brown and John Withers, and boatman Andy Wilson, who helped to make my 300 Antarctic dives easy, productive and (mostly) incident free. Thanks for providing the opportunity to work in such thought-provoking field locations and for not moaning too much about diving in South and Hangar Coves (again!).
- Whilst South, I found a new love of mountains and snowboarding, but not for ice climbing (thanks for trying Tim and Doogs). Special mention to Hamish, Andy, Rob, Ed, and Tim for those special days out on the hill.
- Being away from home for so long gave me a fresh insight into the importance of family. Mum, Dad and Alan, thanks for everything.
- Finally, and most unexpectedly, Antarctica gave me a relationship with the lovely Dr Jo. To her, thanks for your relentless love and support, enthusiastic medical attention and unwavering lust for life. Above all, thanks for saying 'yes'.

The 'writing-up' period based in Cambridge has been both fun and productive. I thank my supervisors (and friends) Keiron Fraser and Dave Barnes for their help and encouragement whilst writing the papers and thesis. Thanks also to Lloyd Peck and Andy Clarke for constructive comments, and to Pete Rothery and Pete Fretwell for assistance with statistics and mapping, respectively.

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DISTURBANCE AND COMMUNITY ECOLOGY

This project aimed to provide novel insights into the influence of ice-mediated disturbance on nearshore benthic communities in Antarctica. Therefore, it seems logical to start the thesis with definitions of both 'disturbance' and 'community', and to remain consistent throughout the work with regards to their meanings.

What is a community?

There have been a number of attempts to define an ecological community, which have varied considerably in their precision. At the loose end of the precision spectrum lie definitions of 'community' such as Poore's (1964) attempt: "...it is an ecological maid-of-all work with undefined duties and responsibilities". Conversely, Hairston (1964) was more specific: "animal communities may be considered organised if any property of a natural assemblage or species can be predicted". More generalised definitions used by modern ecologists perhaps stem from Whittaker's (1975) view: "much ecological understanding can be integrated around the concepts of communities as assemblages of different species which interact with one another, and ecosystems as functional systems formed by communities and their environments". The general concept of a community can therefore be divided into three components, each of which is still debated by ecologists to some degree.

(1) Composition: communities are assemblages of different species living in the same space.

(2) Interaction: species within a community interact with each other and with the physical environment. 'Interactions' between species range from complete interdependence to simply sharing the same general resources, and the study of these relationships has become a key area in community ecology.

(3) Time: the term community implies some degree of permanence (Greig-Smith 1986), although communities generally change through time.

Throughout this thesis the term community will refer to ' a collection of animals and/or plants that occur naturally together, with individuals and populations within the

community interacting with one another and with the abiotic surroundings' (Martin 1976). However, as the study is principally concerned with the distribution of species and not species interactions, biological interactions (i.e. predation, competition, commensalisms) are generally assumed and not actually measured. Therefore, the terms 'community' and 'assemblage' are largely interchangeable in this case.

What is disturbance?

White & Pickett (1985) defined disturbance as 'any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment'. This was a deliberately generalised definition in order to be applicable to all fields of ecology, and disturbances can be further divided into: natural or anthropogenic, destructive events or environmental fluctuations and biological or physical processes. This thesis focuses principally on disturbance of a natural, physical and destructive nature, whilst making comparisons and relating the findings to a broad range of disturbance pressures. When describing disturbance pressures, it is important to consider not only the type of disturbance, but also the spatial distribution, frequency, predictability, severity and scale of each disturbance event (White & Pickett 1985).

Using the above definition, it could be said that disturbance affects every known (metazoan) biological system on Earth. Furthermore, the frequency and magnitude of disturbance events vary considerably between systems and as such natural habitats form a continuum of disturbance pressure. For example, the deep sea habitat and subterranean caves are physically relatively stable and could be described as low disturbance systems (Gage & Tyler 1992, Gibert & Deharveng 2002), whilst shallow water polar habitats and areas of frequent volcanic activity represent the other extreme of the disturbance continuum (Foster et al. 1998, Gutt & Starmans 2001). It is important to note that the frequency and magnitude of disturbance events are not necessarily interrelated and some disturbance pressures are frequent but relatively benign (e.g. spring tides) or conversely, infrequent but potentially catastrophic (e.g. asteroid impacts).

Discrete disturbance events induce heterogeneity in natural communities. Forest fires remove large areas of developed vegetation whilst other areas of forest remain unchanged (e.g. Ahlgren 1974). Hurricanes damage sections of coral reefs (e.g. Connell 1997), lava flows disturb fragments of vegetation (e.g. Eggler 1971) and wave-carried logs and driftwood can destroy patches of rocky shore assemblages (e.g. Dayton 1971). There are countless examples of physical disturbance generating patches of cleared space or altered community structure. Intense disturbance may remove all macroscopic life within a given area, thereby creating primary space and allowing the recommencement of colonisation and successional processes (e.g. intertidal mussel beds, Sousa 1985). One of the most important theories in modern ecology, 'the intermediate disturbance hypothesis' (IDH), suggests that disturbance has a fundamental role in determining and maintaining biodiversity (Connell 1978). The IDH predicts that where disturbance is frequent and/or intense only highly specialised pioneers can persist, whilst in areas of low disturbance, resources may be monopolised by a few top competitors. Thus, where disturbance is intermediate, both pioneer and late successional stages may persist, resulting in increased biodiversity (Connell 1978). Evidence in support of the IDH has come from a number of habitats, including tropical coral reefs (Connell 1978, Rogers 1993), tropical rainforests (Connell 1978, Molino & Sabatier 2001), intertidal boulder fields (Sousa 1979), shallow polar waters (Conlan & Kvitek 2005, Laudien et al. 2007), intertidal rocky shores (Lubchenco 1978), streams (Townsend et al. 1997) and temperate grasslands (Collins et al. 1995).

An important caveat of the IDH is that it relates to patch dynamics and, more specifically, between-patch dynamics of disturbance events within a larger area (White & Pickett 1985, Wilson 1994). To expand, the IDH should not be interpreted as a 'within-patch' mechanism whereby biodiversity is greatest in disturbance patches of intermediate age. Rather, it should be considered a between-patch mechanism where some patches within a given area are in early successional stages and others are in later stages, with each stage supporting a distinct set of species (Connell 1978, Wilson 1994). Therefore, an environment such as the Antarctic shallow subtidal zone, where a number of disturbance patches occur within a single site or region (see below), could be ideal for testing the IDH.

ANTARCTIC BENTHIC COMMUNITIES

Overview

Antarctica is frequently described in the modern media as the 'last great wilderness on Earth' or 'the last frontier', but the number of people living, working and visiting the frozen continent has soared in the last two decades. The number of personnel over-wintering at Antarctic bases is now around 1000, whilst ~30,000 summer workers visit the continent each year (Ward 2007). In addition, the number of Antarctic tourists has quadrupled in the last decade and over 37,000 tourists will enter the Southern Ocean during 2007 (Williams 2007). In the context of benthic marine ecology, the increased number of scientists visiting the continent has intensified sampling effort in recent years, so that regions such as the Antarctic Peninsula and the Weddell and Ross Seas are now fairly well known (Linse et al. 2006, Clarke et al. in press).

Traditionally, the collection of biological material has been largely achieved remotely from research vessels. Sampling of Antarctic benthos commenced well over a century ago, when the first comprehensive biological collections were taken during the Challenger expedition of 1872-1876. Since then, biological research in the Antarctic has evolved steadily and moved on from basic taxonomy to a more holistic approach involving every aspect of biology from genes to ecosystems. Dell (1972), Dayton (1990) and Arntz et al. (1994) provide comprehensive reviews on the history of marine biology in Antarctica.

In addition to remote sampling, a number of Antarctic research stations now support scientific SCUBA diving, which has facilitated (amongst other things) the collection of healthy live specimens for laboratory work, long-term field observations and comprehensive studies of community structure in shallow coastal waters. The first Antarctic SCUBA dive was conducted in 1961 in McMurdo Sound, a site that would later be the focus of the groundbreaking 'under-ice' benthic ecology papers published in the late 1960s and early 1970s (e.g. Dayton et al. 1969, Dayton et al. 1970, Dayton et al. 1974). Today, scientific diving is conducted at ~12 research stations around

Antarctica, with the vast majority of these dives being carried out during the austral summer. All the sampling required for the work presented in this thesis was achieved using standard SCUBA diving techniques (see Heine 1996, and Trotter 2006 for details on Antarctic diving).

The benthos

During the early stages of the ill-fated race for the South Pole in 1912, Captain Robert F. Scott remarked: 'as one looks across the barren stretches of the pack, it is sometimes difficult to realise what teeming life exists immediately beneath its surface'. Perhaps he did not realise the profundity of this observation at the time, but life in the Southern Ocean is indeed remarkably rich and abundant. The diversity of marine benthos around Antarctica is considerably greater than in the Arctic (Arntz et al. 1997, Starmans 1997) and can be comparable to benthic diversity in tropical and temperate zones (Brey et al. 1994, Gray 2001). Some taxa, such as pycnogonids, may even be more diverse in the Southern Ocean than elsewhere (Clarke & Johnston 2003). Also, benthic biomass can be very high in the Antarctic, largely due to great densities of large suspension-feeders (Arntz et al. 1997, Gutt & Starmans 1998).

The Antarctic benthos is also characterised by high levels of endemism in some taxa and the almost complete absence of others, most notably barnacles and reptant decapods (Arntz et al. 1994, Brey et al. 1994, Clarke & Johnston 2003). However, recent studies by Linse et al. (2006) and Barnes and Griffiths (in press) suggest that the levels of endemism in some taxa are not as high as traditionally perceived. Even so, the levels of richness and endemism observed within some taxa are high in the Antarctic relative to elsewhere, and two main explanations have been proposed. Firstly, Antarctica has been isolated for at least 20 million years, following the separation of South America and the Antarctic continent and the formation of Drake Passage (Crame 2000, Clarke et al. 2004). This separation resulted in the formation of the Antarctic Circumpolar Current (ACC), which has acted as an oceanographic barrier and restricted the influx of plankton into the Southern Ocean (Lawver & Gahagan 2003). Consequently, Antarctic marine fauna have existed in some degree of isolation over evolutionary timescales. High allopatric speciation rates due to isolation over time may explain the high species richness and endemism observed in some taxa

today. Furthermore, the Southern Ocean is of considerable size and it is well known that species richness increases with area (MacArthur & Wilson 1967, Gray 2001 and references therein). It is likely that the Southern Ocean encompasses a number of habitats that provide a countless number of ecological niches, and a high diversity of species have evolved to fill them.

Ice disturbance

Physical disturbance by ice is a major structuring force acting on polar benthic communities over both evolutionary and ecological timescales. Since the isolation of Antarctica the extent of continental glaciation has varied greatly, particularly during the last 2 million years as glacial ice has advanced and retreated cyclically (Williams et al. 1998). During glacial maxima, ice extended northwards and into deeper water, forcing continental shelf fauna down into the deep continental margins (Clarke & Crame 1992). The extent of the shelf defaunation is unclear and there is some evidence to suggest the existence of undisturbed refugia, which may have acted as both source communities for subsequent recolonisation (Brey et al. 1996) and hotspots for allopatric speciation (Held 2003, Allegrucci et al. 2006). During interglacial periods, the shallow continental shelf became ice-free and was subsequently recolonised by source communities in deeper water or from isolated refugia. Thus, most Antarctic marine habitats are currently in some stage of recolonisation.

On ecological timescales, the effects of ice disturbance are largely dependent on the type of ice creating the disturbance pressure. Anchor ice forms at high latitudes where super-cooled water freezes around objects on the seabed, such as stones and biota. As the platelet ice expands it becomes increasingly buoyant and can rip ice-encased fauna and flora from the seabed (Dayton et al. 1969). A mass of 25 kg can be lifted from the seabed by anchor ice (Picken 1984). Anchor ice generally occurs during winter in the shallow sublittoral zone (up to 30 m depth) and can result in a near denudation of sessile fauna at very shallow depths and clear depth-dependent patterns in species distributions (Dayton et al. 1970, Dayton et al. 1974). Although anchor ice disturbance can be intense, it is restricted to high latitude locations with suitable

oceanographic conditions and is not as widespread as disturbance from icebergs, sea ice floes and the ice foot.

Ice scouring occurs when floating ice, either glacier-derived (icebergs) or ocean-formed (sea ice), impacts the seabed. Ice scouring may result in considerable physical alterations to the seabed, the resuspension of deposited sediment and changes in water movements (Rearic et al. 1990, Woodworth-Lynas et al. 1991). In ecological terms, ice scouring can be catastrophic (Peck et al. 1999) and its effects include skewed population structures (Peck & Bullough 1993, Brown et al. 2004), elevated abundances of secondary consumers (Richardson & Hedgepeth 1977, Conlan et al. 1998), niche separation (Brenner et al. 2001) and the persistence of early successional stages (McCook & Chapman 1993, Pugh & Davenport 1997). It has been suggested that the intensity of ice scouring decreases with depth and therefore drives depth-dependent species distributions in shallow polar waters (e.g. Lenihan & Oliver 1995, Nonato et al. 2000, Barnes & Brockington 2003). However, this has not been empirically tested and remains one of the most widely used paradigms in polar marine ecology.

Ice scouring is a widespread phenomenon and may affect up to one fifth of the world's coastlines (Gutt & Starmans 2001). It can also be frequent; an estimate based on relict scour marks and the growth rates of pioneer species suggested that on average each square metre of the Antarctic shelf (to 500 m depth) is disturbed by ice once every 340 years (Gutt & Starmans 2001). Studies on the ecological effects of ice scouring have been carried out in Arctic locations such as West Spitsbergen (Laudien et al. 2007) and the Canadian Arctic (Conlan et al. 1998, Conlan & Kvitek 2005) and at a number of Antarctic sites, including the South Orkney Islands (Peck et al. 1999), the Weddell Sea (Gutt et al. 1996, Gerdes et al. 2003) and McMurdo Sound (Lenihan & Oliver 1995).

At high latitudes the intertidal and immediate subtidal zones are also disturbed by the ice foot, which forms during winter where the sea (fast) ice meets the shoreline. The ice foot encapsulates rocky substrata and associated biota, restricting gas and water exchange and reducing the ambient temperature towards air temperature. As a result, the surfaces of polar intertidal zones are generally denuded of macro-biota and species

poor, with colonisation of substrata restricted to a few months during the ice-free summer (Stockton 1973, Zamorano 1983, Barnes 1995b). However, in environments such as intertidal boulder fields, protected microhabitats can support an unexpected wealth of species and individuals, some of which survive winters and form simple communities (Waller et al. 2006). Barnes (1999), Gutt (2001) and Barnes and Conlan (2007) provide comprehensive reviews on the ecological effects of ice disturbance.

AIMS OF THE CURRENT STUDY

The principal aim of this research was to test the widely used paradigm that ice-mediated disturbance structures nearshore benthic communities in Antarctica. The research aimed to address three main questions:

1) Is there any evidence of community change along environmental gradients in the study region?

2) If ice disturbance is a driving force influencing patterns of community structure, what are the direct effects of a disturbance event?

3) Does the intensity of ice disturbance determine community structure?

The first question is, in effect, a prerequisite for addressing the main aim of the research. One cannot test the theory that physical pressures influence the distribution of species if there is no evidence of a heterogeneous distribution of assemblages at the study location. There are many reports of nearshore benthos being distributed along a bathymetric gradient from other Antarctic locations (e.g. Gruzov et al. 1967, Zamorano 1983, Gambi et al. 1994, Barnes 1995c, Sahade et al. 1998), but currently there are only two reports of community change along a depth/disturbance gradient from Adelaide Island (Barnes & Brockington 2003, Bowden 2005a). Both studies provided some evidence for depth-dependent distributions of assemblages, but both had insufficient replication to fully assess the effects of depth and site, which could be useful proxies for disturbance intensity, on patterns of community change.

The second question relates to the small-scale effects of ice disturbance. In the Antarctic, iceberg groundings may be catastrophic at small scales and can result in high benthic mortality and major alterations to community structure. To date, shallow water iceberg scours have been sampled at the South Orkney Islands (Peck et al. 1999) and at McMurdo Sound (Lenihan & Oliver 1995), but there are currently no studies involving multiple scours at contrasting sites. Furthermore, the initial stages of post-disturbance recovery within iceberg scours have been monitored in just one Antarctic iceberg scour (Peck et al. 1999). This section of study aimed to assess the immediate impact of iceberg scouring on shallow water benthos at contrasting sites, and to monitor the subsequent recovery of scour assemblages in a number of scours.

To address the final question, the development of a robust and reliable field technique to quantify the frequency and intensity of ice disturbance was first required. Two previous attempts have been made to quantify ice scouring (Brown et al. 2004, Scrosati & Heaven 2006), and the aim of the current study was to develop these techniques further to generate a detailed data set of ice disturbance frequencies. These disturbance data could then be linked with biological parameters to test empirically the relationship between ice disturbance and Antarctic benthic community structure for the first time.

Post-disturbance recovery in Antarctic communities is thought to be a slow process, principally because of slow recruitment, development and growth rates (Arntz et al. 1994, Stanwell-Smith & Barnes 1997, Peck 2002, Bowden et al. 2006, Barnes et al. 2007). Therefore, it was apparent from the inception of the project that it would not be possible to monitor the complete recovery of benthic assemblages following ice scouring. However, it was clear that a detailed assessment of the immediate effects of ice scouring and the early stages of post-disturbance recovery would be a novel, and therefore important, contribution to polar marine ecology. In addition, even though marine biologists had been diving at study sites around Adelaide Island since 1997, the benthos at many sites had not been described in any detail and background levels of richness and abundance were unknown. Whilst fulfilling the principal purpose of the study, it was hoped that the work would also increase understandings of the taxonomic richness at this remote polar location.

Chapter 2 – The study sites

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REGIONAL DESCRIPTION

All fieldwork for this project was carried out from Rothera Research Station, the largest of the British Antarctic Survey's (BAS) research stations. The research station is situated on a rocky outcrop (Rothera Point) on the southeast coast of Adelaide Island, West Antarctic Peninsula (67° 34.5′ S, 68° 07.0′ W, Figure 2.1). The area is mountainous- the highest peak on Adelaide Island stands at 2565 m above sea level- and this is reflected in the coastal seabed topography, which is dominated by steep rocky substrata. During the study period, monthly mean air temperatures at Rothera Point ranged from –22.1°C to 0.6°C and at this latitude the sun remains below the horizon for ~8 weeks during winter. The prevailing wind at Rothera is from the north (mean wind direction from monthly averages during the study period: 006°) and may reach speeds in excess of 80 knots (41 ms^{-1}) during storm events (all meteorological records are BAS unpublished data).

The coastal waters of Adelaide Island are intensely seasonal, and therefore typical of Antarctic nearshore environments (Whitaker 1982, Clarke 1988). Oceanographic measurements taken in Ryder Bay (the area of water to the southwest of Rothera Point) since 1997 show that primary productivity follows a distinct seasonal pattern (Figure 2.2), which is driven by changes in solar radiation throughout the year. The seasonal bloom in phytoplankton has a direct and wide-ranging influence on the ecology of both benthic (Barnes & Clarke 1995, Brockington et al. 2001, Fraser et al. 2002) and pelagic invertebrates (Everson 1984, Schnack-Schiel & Hagen 1994), as well as migratory vertebrates (Laws 1977, Brown & Lockyer 1984).

In addition to seasonal cycles in primary production, seasonal changes in seawater temperature also occur at Adelaide Island, although the annual temperature range is small compared with lower latitudes (<4°C at 15 m depth, Figure 2.2). Furthermore, due to the formation of fast ice during winter, which restricts iceberg movements and reduces wind-induced water movements, the intensity of physical disturbance may also be seasonal (Clarke 1988, Barnes 1999).

Figure 2.1 The Antarctic Peninsula showing the position of Rothera Research Station on Adelaide Island.

The waters around Adelaide Island are heavily laden with ice. The immediate area is well glaciated and large ice shelves lie to the south; hence iceberg loading into coastal waters in this region is likely to be high. Also, during winter most of the region is covered in fast ice and the intertidal environment is covered by an ice foot (reports of anchor ice formation are very rare). As a result, the nearshore habitats at Adelaide Island are subject to disturbance by a number of different forms of ice, each of which may have a different influence on the ecology of the benthos. Therefore, throughout this thesis each form is referred to specifically, using accepted definitions from the World Meteorological Organisation (Table 2.1). Movement of ice around the region is influenced by strong winds (predominately from the north) and water movements, which in turn are influenced by a complex semidiurnal tidal pattern and oceanic currents circling Ryder Bay.

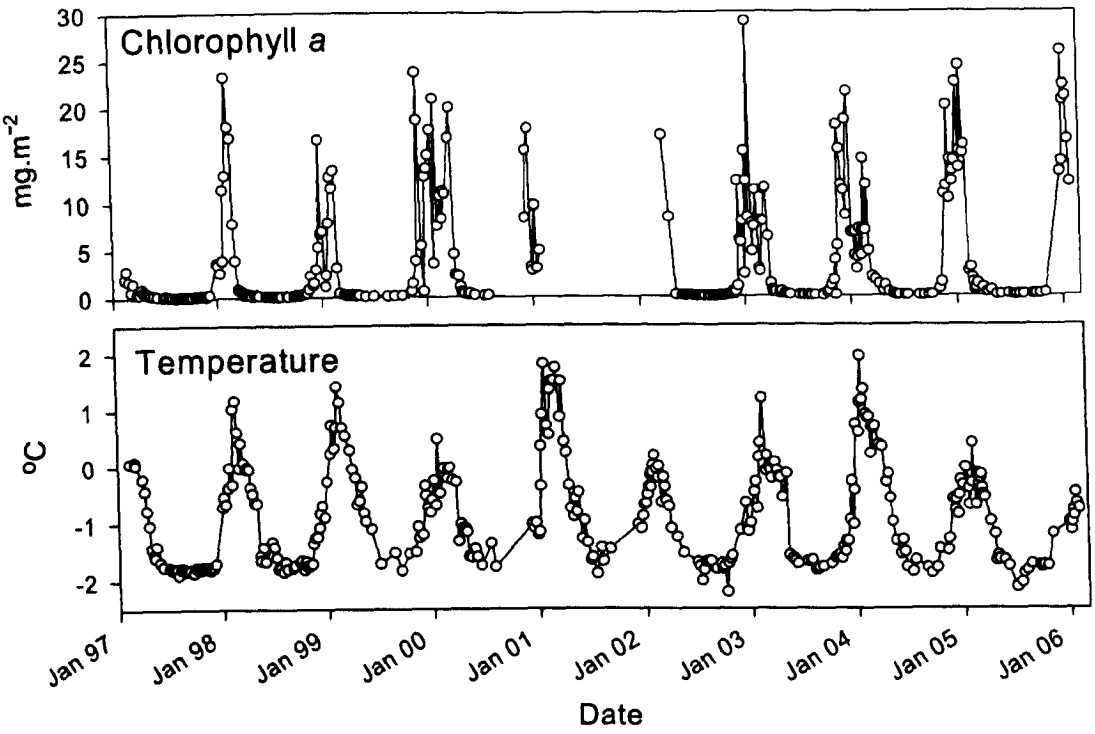


Figure 2.2 Total chlorophyll a concentrations and seawater temperatures at 15 m depth in Ryder Bay from February 1997 to February 2006. Data were collected as part of a long-term monitoring programme at Rothera Research Station (BAS unpublished data).

Table 2.1. Types and definitions of sea ice observed at study sites at Rothera Point, Adelaide Island, West Antarctic Peninsula. Adapted from Haykin et al (1994) and the World Meteorological Organisation (WMO 1970).

ICEBERGS			
Type	Height above waterline (m)	Relative size	Mass (tonnes)
Iceberg	>5	Merchant ship	180,000
Bergy bit	1-5	Small house	up to 5400
Growler	<1	Grand piano	up to 120
Brash	-	Car tyre	<1

SEASONAL SEA ICE	
Type	Definition
Fast ice	Consolidated solid ice attached to the shore, to an ice wall or to an ice front.
Ice foot	A narrow fringe of ice attached to the coast, unresponsive to tidal oscillations.
Sea ice floe	Any relatively flat (free floating) piece of sea ice more than 20 m across.

STUDY SITES

In total, sampling was conducted at five different study sites, all within close proximity to Rothera Research Station (Figure 2.3). However, the majority of the work was conducted at the two coves adjacent to the station, South Cove and Hangar Cove (Figure 2.3). These coves were selected for three reasons: (1) a preliminary study by Brown et al. (2004) indicated that both these sites were subject to frequent disturbance from ice scouring. (2) A major component of the research required sites to be visited regularly throughout the year; these sites are readily accessible during most ice and weather conditions. (3) Since the commencement of scientific diving at Adelaide Island in 1996 South Cove and Hangar Cove have been the most frequently visited field sites. As a result, BAS scientists were familiar with some of the more abundant and conspicuous fauna at these sites.

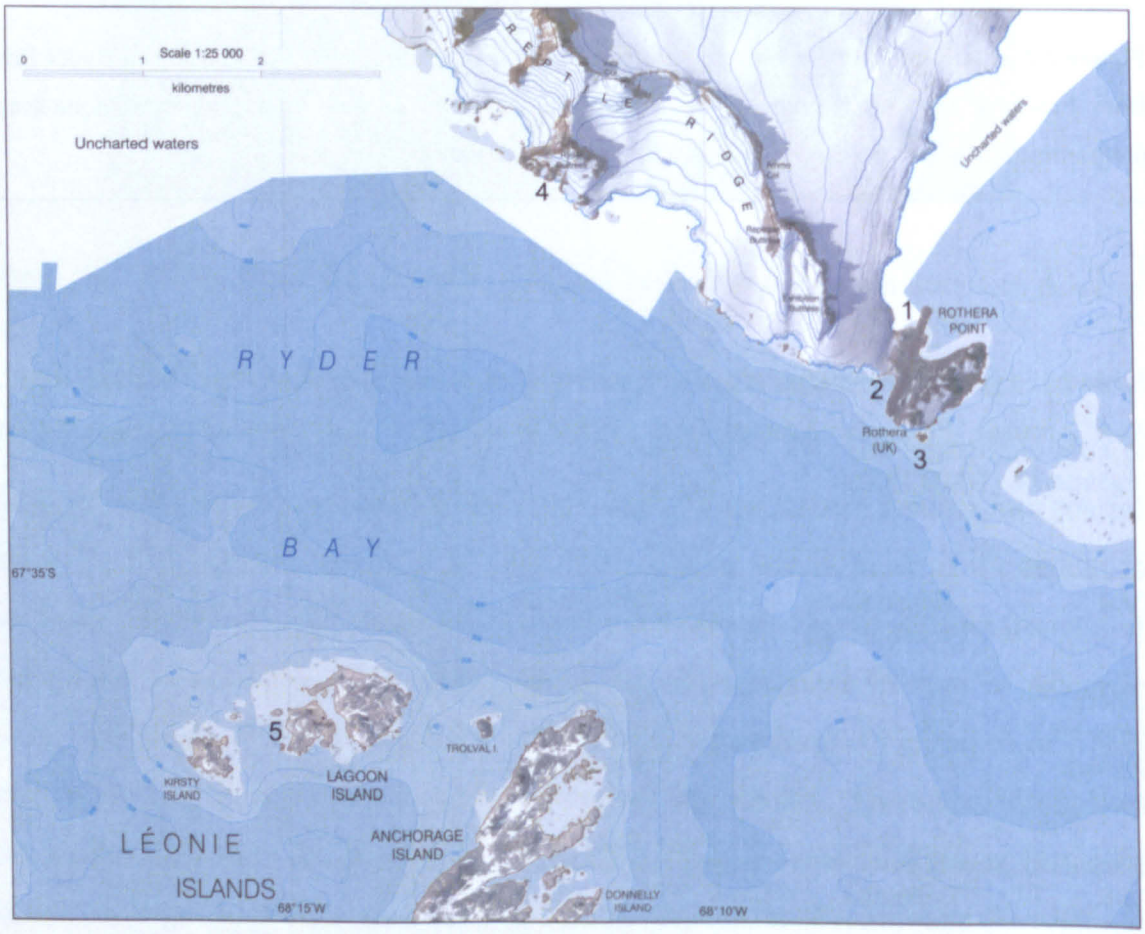


Figure 2.3 The southeast coast of Adelaide Island showing Rothera Point and Ryder Bay. The five study sites are shown: (1) Hangar Cove (2) South Cove (3) Cheshire Island (4) Ryder Buttress (5) Lagoon Bay.

South Cove is southwest facing inlet covering a surface area of ~0.05 km^2. The Rothera airstrip, built in 1991, runs to the east of the cove and the ice cliffs of the Wormald Ice Piedmont mark the western boundary of the inlet. Most of South Cove has a constant incline of ~30° from the horizontal, although the gradient increases considerably at the southern end of the cove. The substratum at South Cove is primarily a mixture of hard bedrock and areas of compacted cobbles, with isolated patches of fine sediment. Tidally induced currents are slow to moderate but frequently push brash ice and icebergs into the cove during calm weather (personal observation). Due to the prevailing northerly wind direction of the region, South Cove is often free of ice during the summer months as brash ice, icebergs and sea ice flows are frequently blown southwards. Records collected at the site since 1997 show that fast ice forms in early winter and persists for a variable period of 1-7 months, depending on a number of climatic and oceanographic factors (Figure 2.4) (Wadhams 2000). To date, two comprehensive surveys of the benthos at South Cove have been published. Benthic assemblages, both macrofaunal and cryptofaunal, are rich and abundant and demonstrate considerable change along a bathymetric gradient (Barnes & Brockington 2003, Bowden 2005a).

The other main study site, Hangar Cove, has a number of characteristics in common with South Cove. Hangar Cove covers a similar area, is also bounded by the Rothera airstrip to the east and steep ice cliffs to the west, and has a consistent incline of ~30° from the horizontal. The two sites differ primarily in substratum type and aspect. Hangar Cove is a soft-sediment habitat; a base of compacted cobbles is covered with a layer of silt that varies in thickness from 0 to ~20 cm. Furthermore, Hangar Cove has a northeast facing aspect and is therefore exposed to the prevailing wind. As a result, the site is often packed with wind-blown ice during the summer months. Icebergs, bergy bits and brash ice are frequently observed grounded at depths of 0-40 m during the summer months (personal observation). Fast ice also forms at this site during the winter months, but generally forms earlier and persists for longer periods compared with South Cove (Figure 2.4). Between January 1997 and January 2006, fast ice was recorded at Hangar Cove ~1.5 times more frequently than at South Cove.

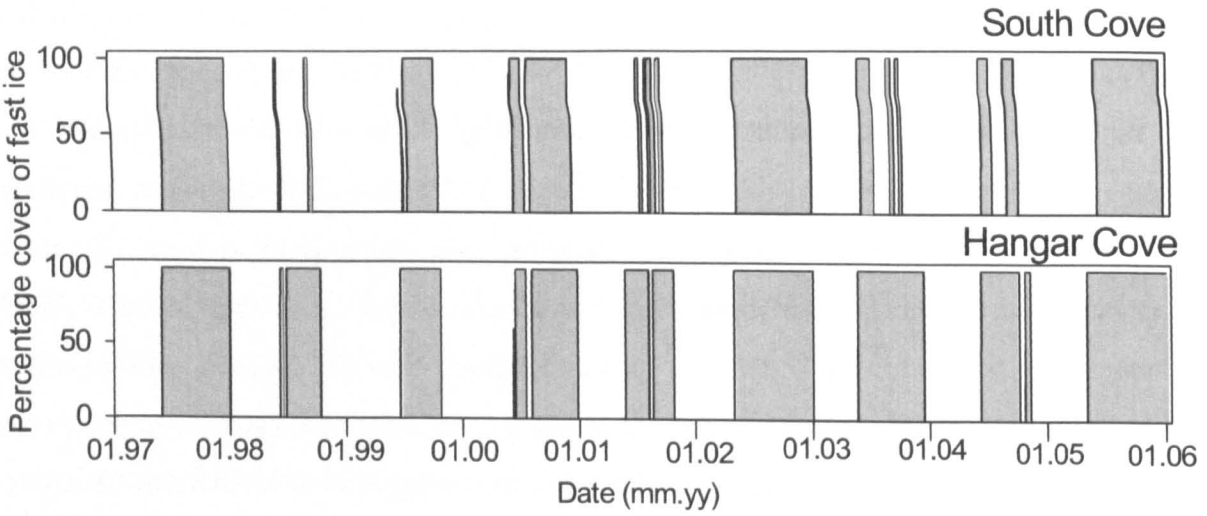


Figure 2.4 Periods of 100% cover of fast ice (grey bars) at South Cove and Hangar Cove between January 1997 and January 2006. Data were collected as part of a long-term monitoring programme at Rothera Research Station (BAS unpublished data).

Although both study sites were directly adjacent to Rothera Research Station, anthropogenic contamination from the station is both minimal and localised (Lohan et al. 2001, Hughes 2004). Therefore, apart from the physical disturbance from the construction of the airstrip in 1991, the sites and the assemblages they support are largely uninfluenced by man.

In addition to the main study sites, depth-related patterns of community change were investigated at Cheshire Island and Ryder Buttress (Chapter 3) and recent iceberg scours were sampled at Lagoon Bay (Chapter 4). Descriptions of these sites are presented within the relevant chapters.

Chapter 3 – Benthic community structure at Adelaide Island

The data in this chapter are also published as: Smale D. A. (in press) Continuous benthic community change along a bathymetric gradient in nearshore Antarctica: evidence of patchiness but not zonation. Polar Biology. Online First DOI: 10.1007/s00300-007-0346-3.

Chapter 3 – Benthic community structure at Adelaide Island

INTRODUCTION

In the past half-century, Antarctic benthologists have presented strong evidence to suggest the existence of depth-dependent distribution of organisms in shallow nearshore waters (i.e. 0-60 m depth). Following the development and employment of SCUBA diving techniques in the 1960s, a range of photographic, coring and collection techniques have been used to sample nearshore Antarctic benthos. To date, at least 30 published studies from around Antarctica conclude that benthic community structure in shallow subtidal zones changes along a bathymetric gradient (Fig. 3.1). Ice-mediated disturbance, in the form of iceberg scouring (Peck & Bullough 1993, Sahade et al. 1998, Nonato et al. 2000), encapsulation by the ice foot (Waller et al. 2006) or the action of anchor ice (Dayton et al. 1969, Dayton et al. 1970), have been frequently suggested as the driving force behind the depth-dependent distribution of benthos.

Recently, attempts have been made to quantify the frequency and intensity of disturbance by ice in the shallow subtidal zone. Communities exposed to iceberg groundings at ~10 m depth may be impacted more than once a year (Brown et al. 2004) but the frequency of disturbance events is thought to decrease with depth. Therefore, it is likely that in shallow subtidal zones ice disturbance structures the benthos, whilst at depths below ~30 m biological factors such as competition and predation become prevalent in determining organism distribution (Dayton et al. 1974, Sahade et al. 1998). Antarctic communities may, however, be highly variable and patchy (Gutt & Starmans 1998, Gutt & Piepenburg 2003) and other physical factors that may influence community structure include substratum (Kirkwood & Burton 1988, Barnes 1995c), input of phytoplankton (Dayton & Oliver 1977), contamination (Lenihan & Oliver 1995, Conlan et al. 2004) and current flow (Ragua-Gil et al. 2004).

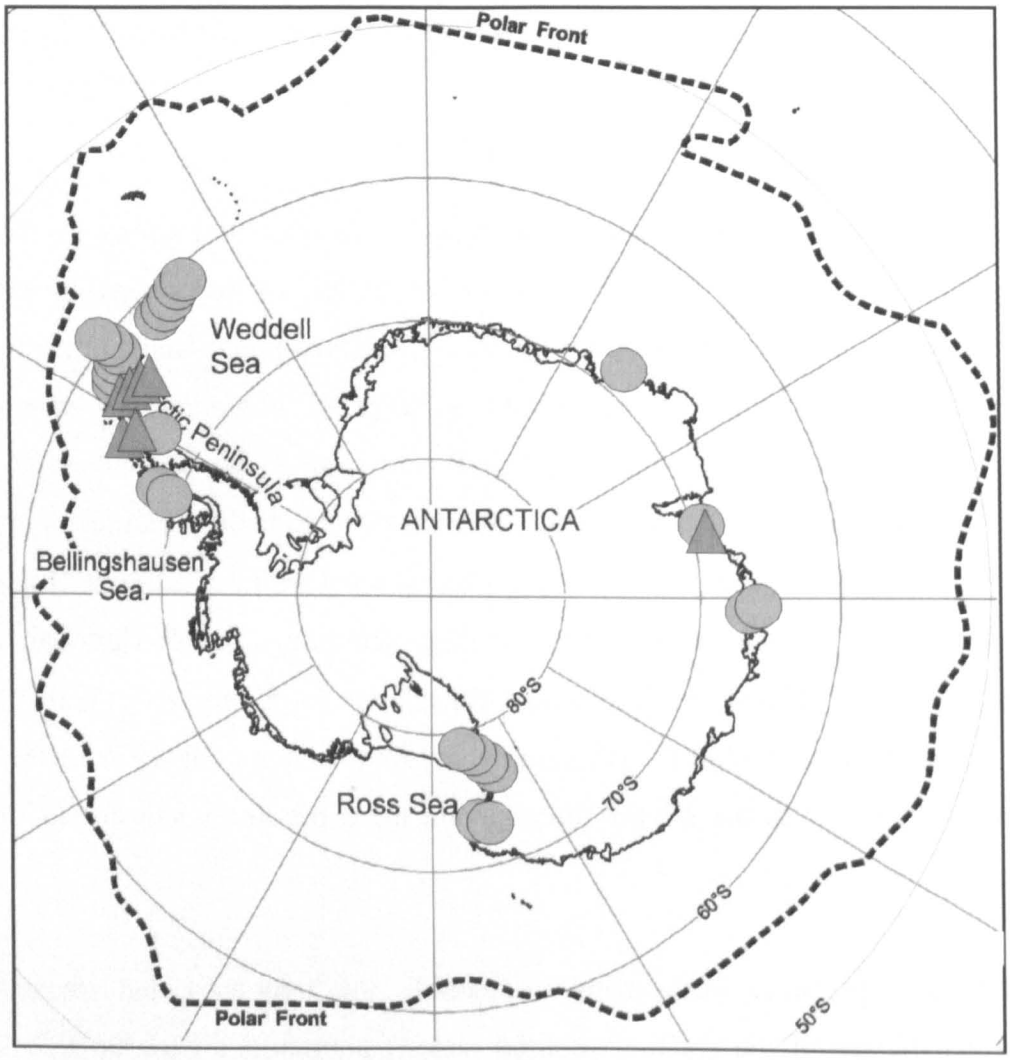


Figure 3.1 Locations of studies suggesting that benthic community change occurs along a bathymetric gradient in Antarctic shallow subtidal zones (0-60 m depth). Circles represent studies that used SCUBA diving sampling techniques, whilst triangles indicate studies with remote sampling protocols (grabs, cores and suction pumps).

Despite the widely accepted notion that coastal Antarctic benthic community structure changes along a bathymetric gradient, there are currently very few studies with acceptable replication at the sample, transect and site level of study. Furthermore, in respect to assessing community change along a bathymetric gradient, there have been no applications of powerful multivariate analyses, which have become valuable tools for modern ecologists studying natural systems (James & McCulloch 1990, Clarke 1993, Jackson 1993). The current study aimed to test the following hypotheses: (1) the abundances of species, phyla and structural forms change along a vertical (bathymetric) gradient in nearshore Antarctic waters, (2) assemblages change along a

continuum and do not form discrete boundaries or zones, (3) due to the stochastic nature of ice disturbance, horizontal patchiness across the bathymetric gradient is significant.

METHODS

Study sites

Sampling was conducted at three sites, Cheshire Island, South Cove and Ryder Buttress. The sites were chosen as they had a number of similar characteristics; slopes with a south-facing aspect, comparable current flows and primarily hard bedrock substrata with patches of semi-stable cobbles and overlying silt. The three sites differed markedly in the gradient of the topography; Cheshire Island had a constant but gently sloping depth profile, Ryder Buttress was an almost vertical cliff face with numerous overhangs and crevices, whilst South Cove had an intermediate gradient. These pronounced differences in topography may have offered benthos differing degrees of protection from ice disturbance.

Sampling protocol

Three replicate transects, running from 5 m to 35 m depth, were sampled at each site. Transects at each site ran parallel to each other, ~10 m apart. The maximum depth and separation distance of transects were determined by SCUBA diving restrictions. Cheshire Island and South Cove were sampled through winter fast ice during October 2005, Ryder Buttress was sampled in January 2006. Transects were sampled at 7 stations, each at 5 m depth intervals. At each station (there were 63 in total) 10-15 photoquadrats were taken; SCUBA divers placed the camera with closed eyes. From this pool of photoquadrats 8 were chosen, at random, for analysis.

A Nikon D100 digital SLR camera fitted with Nikkor 12-24 mm (set at 24 mm) DX lens was housed in a Nexus D100 casing and used throughout. Lighting was produced by a single Nikonos SB105 flash unit fitted with a diffuser. A carbon fibre framer was used to standardise the sample area and to ensure the camera remained perpendicular to the seabed. Each image was cropped to a sample area of 0.32 m^2 and all discernible fauna >5 mm in length were identified to the lowest possible taxonomic level, which was generally species (hydroids and pycnogonids were less discernible). All individuals of solitary taxa were counted, whilst modular taxa (sponges, hydroids,

bryozoans and some ascidians) were quantified by the number of colonies or units. Some components of the biota were excluded from analysis: encrusting taxa (some smaller bryozoans and sponges, spirorbid and serpulid worms) could not be accurately identified and quantified; although conspicuous at other Antarctic locations, macrophytes were neither speciose nor abundant at the study sites and were not quantified; fish were not included in the analysis.

Data analysis

The partitioning of variation in total abundance and species richness was examined with a balanced ANOVA in Minitab 14.0. Transects were treated as random and nested within sites, depth was a fixed factor. Examination of residuals suggested that data should be log transformed prior to analysis to decrease heterogeneity of variance. Data presented in figures were pooled for each depth station to give a sample area of 2.56 m^{-2} and then averaged across the three replicate transects within each site (± standard error).

Multivariate analyses were applied using the Primer v.6 (Primer-e Ltd. Plymouth, UK) statistical software. Replicates for each depth station were initially pooled and then square root transformed, to down-weight the importance of the highly abundant limpet *Nacella concinna* and echinoid *Sterechinus neumayeri*. A Bray-Curtis similarity matrix was then generated and was used to produce MDS (non-metric multidimensional scaling) plots with site and depth factors. Two-way ANOSIM tests were then applied to test the significance of the observed groupings. Finally, the taxa contributing most to the dissimilarity between depth groups were determined by applying the SIMPER procedure. Finally, the RELATE procedure was applied to determine the correlation between the abundance similarity matrices from each site and a model matrix of vertical distance between samples.

RESULTS

Changes in community structure with depth

In total 504 photoquadrats, covering an area of ~160 m^2, were analysed. More than 41,000 animals, representing 10 phyla and at least 75 species, were counted. A significant interaction between depth and site was recorded for both total abundance and species richness, suggesting that the magnitude of differences were not consistent across sites (Table 3.1). An examination of plots showed that patterns at Ryder Buttress differed from those observed at the other sites, but only in the magnitude of change and not the direction of change (Fig. 3.2). Interactions notwithstanding, total faunal abundance significantly differed between depth stations and transects (Table 3.1). The density of animals was greatest in the shallows (5 m and 10 m depth) at every site. The greatest faunal abundance was recorded at Cheshire Island at 5 m depth where 1737 ± 220 inds.2.56m^{-2} were recorded. Total abundance decreased markedly from 5 m to 15 m depth at Cheshire Island and South Cove and thereafter remained consistent at the deeper depth stations (Fig. 3.2). At Ryder Buttress, the density of animals was lower compared with the other study sites, particularly in the shallows, and remained relatively constant along the depth transects (Fig. 3.2). Species richness was significantly different between depth stations (Table 3.1) and showed a general increase with depth at all sites, although this relationship was strongest in the shallower stations of the transects (Fig. 3.2). Richness at the coarser taxonomic level of phylum, also increased with depth but reached asymptotes at shallower depths compared with species richness curves; phylum richness increased markedly between 5 and 15 m depth and levelled off at 20-25 m at all sites (Fig. 3.2).

Changes in the relative abundance of dominant phyla along the bathymetric gradient were largely consistent across the study sites. Molluscs (dominated by *Nacella concinna*) decreased in abundance along depth transects whilst bryozoans and sponges were absent from all 5 m and 10 m depth stations and then increased in abundance from 15 m to 35 m (Fig. 3.3). At the 35 m depth stations bryozoans were a dominant component of the benthos, comprising 37 ± 3%, 40 ± 2% and 18 ± 3% of total faunal abundance at Cheshire Island, South Cove and Ryder Buttress,

respectively. Echinoderms were consistently a dominant group at all sites, but showed no consistent pattern with depth (Fig. 3.3).

Table 3.1 Results of balanced ANOVA with (log transformed) total abundance and species richness response factors. Transects were nested within sites and treated as random factors.

Total abundance (log transformed)

Source	DF	SS	MS	F	P
site	2	4.6339	2.3170	1.20	0.364
transect(site)	6	11.5634	1.9272	3.26	0.012
depth	6	40.9301	6.8217	11.52	0.000
site*depth	12	19.0700	1.5892	2.68	0.011
depth*transect(site)	36	21.3141	0.5921	5.96	0.000
Error	441	43.8307	0.0994		
Total	503	141.3422			

Species richness (log transformed)

Source	DF	SS	MS	F	P
site	2	3.1264	1.5632	5.84	0.039
transect(site)	6	1.6070	0.2678	1.02	0.430
depth	6	171.2033	28.5339	108.28	0.000
site*depth	12	6.7130	0.5594	2.12	0.040
depth*transect(site)	36	9.4863	0.2635	5.13	0.000
Error	441	22.6495	0.0514		
Total	503	214.7855			

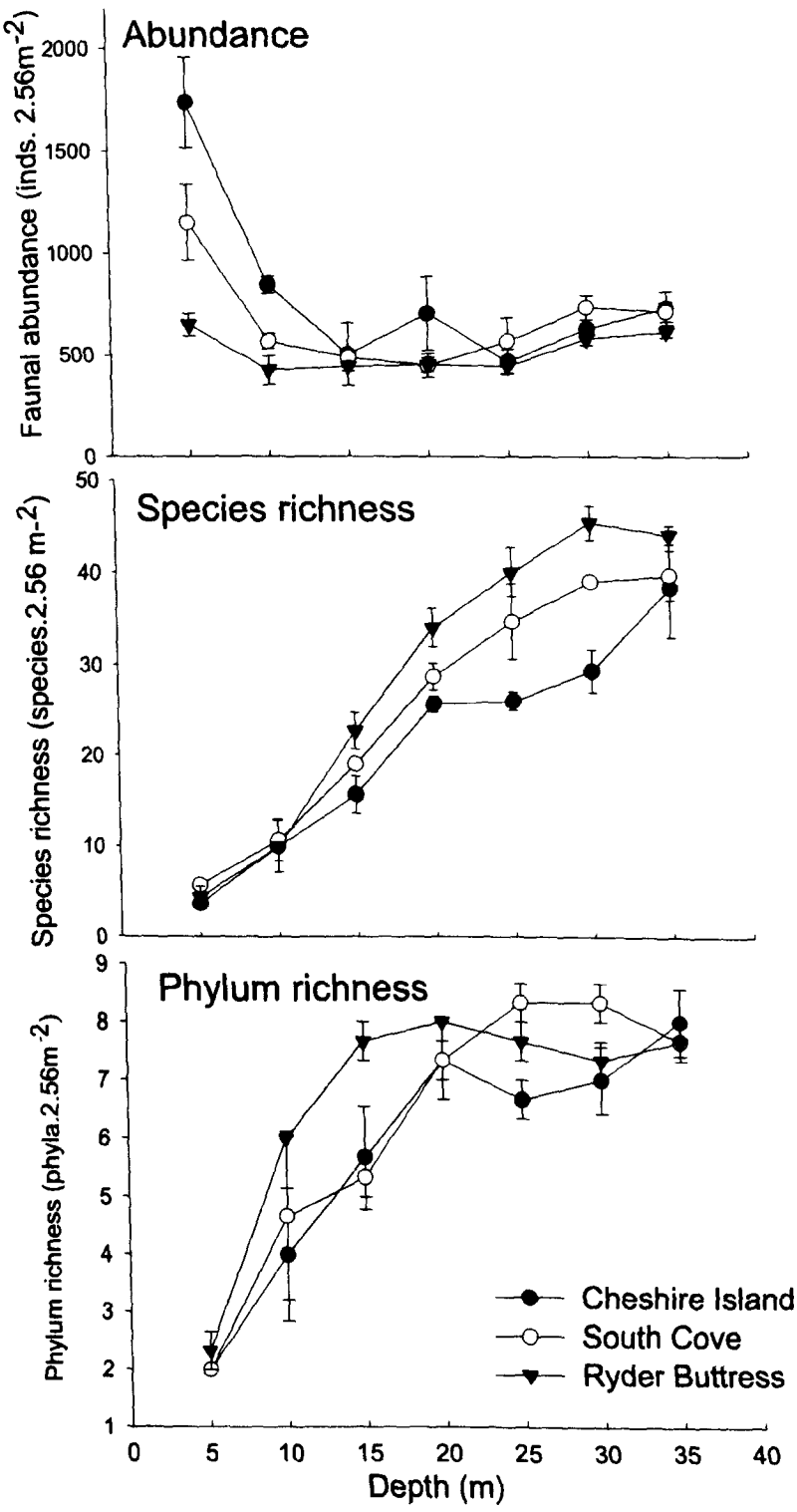


Figure 3.2 Faunal abundance and richness at the species and phylum level at each depth station at each site. Data are means of three transects (± SE).

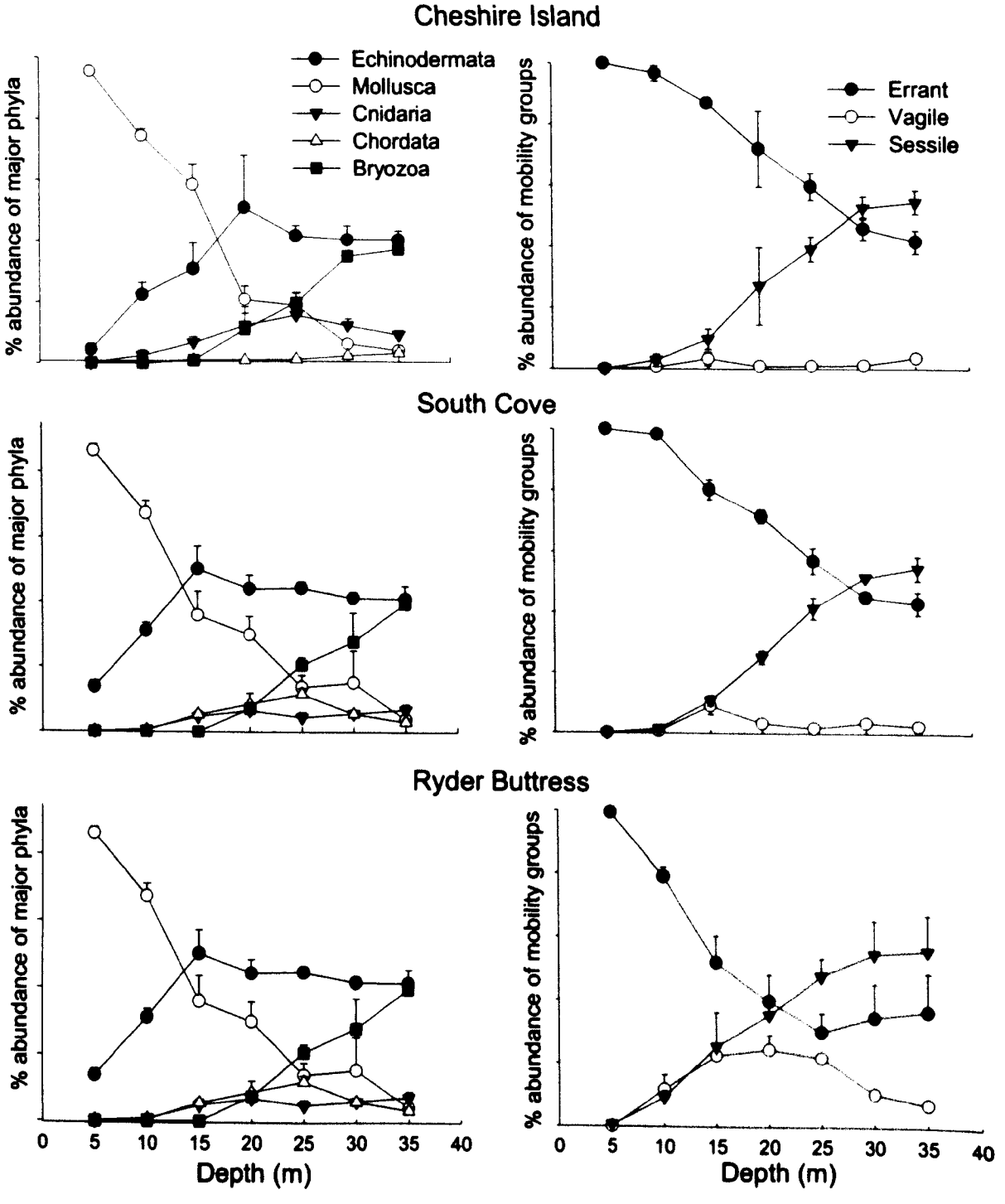


Figure 3.3 Percentage abundance of major phyla (left) and mobility groups (right) at each depth station at each site. Data are means of three transects (± SE).

All fauna were classified into three mobility groups; errant animals were those that moved to feed (mainly asteroids, ophiuroids, echinoids and gastropod molluscs); vagile were those that could move (slowly) but generally maintain a position whilst suspension feeding (holothurians and terebellid polychaetes); and finally sessile fauna, which were attached to the substrata (mainly bryozoans, ascidians and sponges). The relative abundance of these mobility groups showed a distinct pattern along the depth transects at all study sites. In the shallows (5 m and 10 m depth stations) at all sites errant fauna dominated assemblages, but this dominance decreased with depth until at the deepest stations (35 m) more than half of the animals observed were sessile (Fig. 3.3). Cheshire Island and South Cove had very similar patterns in the relative abundances of motility groups. At both sites the sessile group became the most abundant group at 30 m depth, and the vagile group had relatively low abundance values (Fig. 3.3). At Ryder Buttress, however, the sessile group became most abundant at 25 m depth and the vagile group was consistently more abundant, peaking at a 25 ± 5% of the total abundance of animals at 20 m depth (Fig. 3.3).

Continuous community change

Multivariate analyses showed that benthic assemblages were significantly different at each site (Global ANOSIM R = 0.873, $P = 0.01$, 999 permutations) and that, overall, depth stations were highly dissimilar to each other in terms of the abundances of both species (Global ANOSIM R = 0.806, $P = 0.01$, 999 permutations) and phyla (Global ANOSIM R = 0.724, $P = 0.01$, 999 permutations). Although each site supported a distinct assemblage, patterns of assemblage change within each site were similar (Fig. 3.4). MDS ordinations for each site showed clear seriation of assemblages along the bathymetric gradient, so that assemblages were not clustered into distinct depth zones, but were broadly arranged along a trajectory of increasing depth (Fig. 3.4). Ordinations using the abundances of phyla showed a similar pattern. Adjacent depth stations at the shallow ends of transects were generally more separated than those at the deepest depth stations, indicating that communities at 25-35 m depth were more homogeneous than those at 5-15 m depth (Fig. 3.4). The ANOSIM R values from pair-wise tests were highly variable between sites and depth groupings, perhaps due to a low number of possible permutations when testing within each site, but they do

suggest that dissimilarity is greater between adjacent depth groups in the shallows (e.g. 5 and 10 m depth) than at deeper stations (e.g. 30 and 35 m depth) (Fig. 3.5). When testing across all sites, and therefore increasing power and significance from the number of permutations, a general decrease in the dissimilarity between adjacent depth groups was observed with an increased depth (Fig. 3.5).

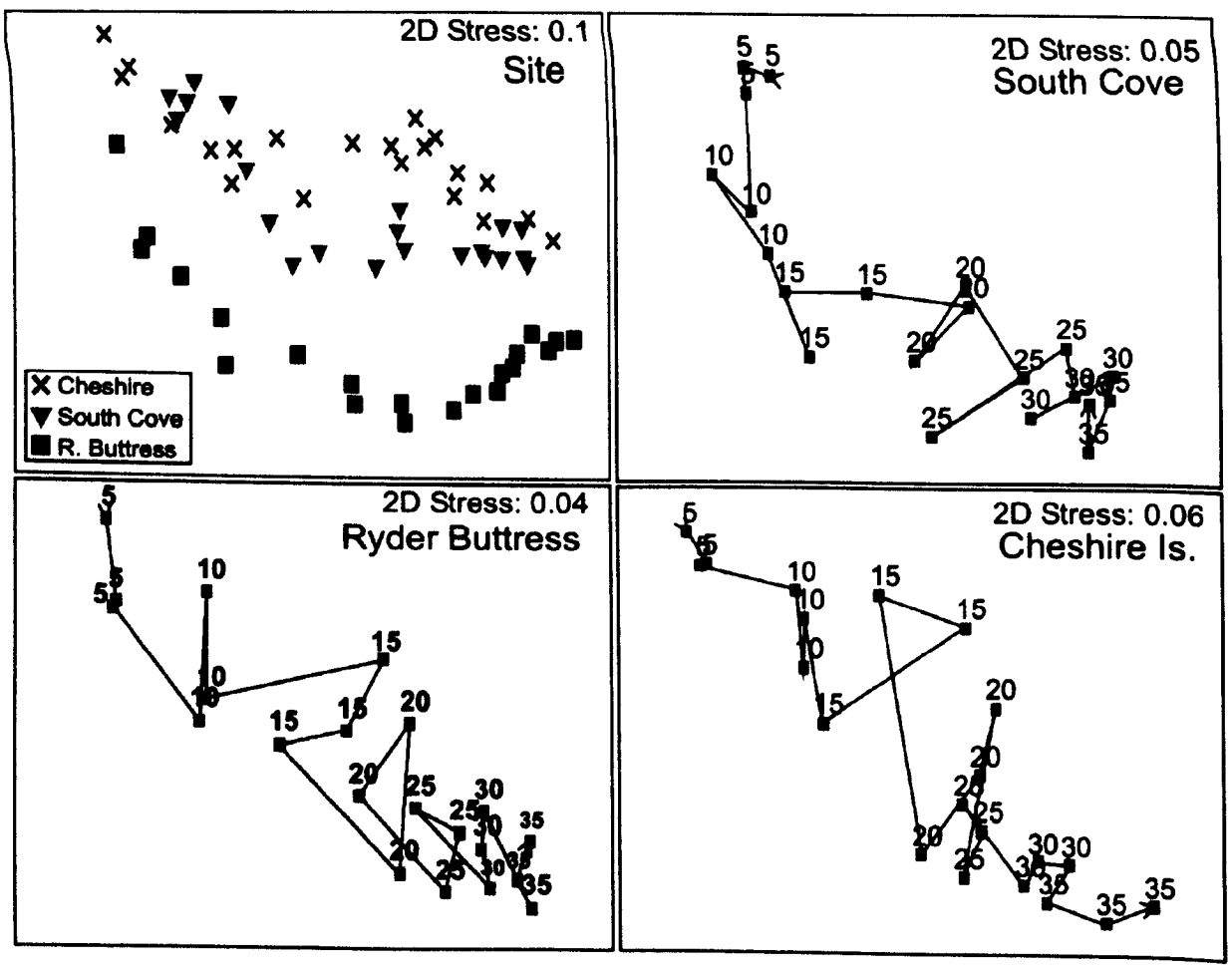


Figure 3.4 MDS ordinations of depth groups at each study site and overall plot of all stations and sites. MDS plots generated from Bray-Curtis similarity matrix of square-root transformed abundance data.

At all sites, a RELATE test showed a significant correlation between the similarity matrix generated from species abundance data and a model matrix of differences in depth between sampling stations (Cheshire Island; $\rho = 0.905$, $P = 0.01$, South Cove; $\rho = 0.904$, $P = 0.01$, Ryder Buttress; $\rho = 0.861$, $P = 0.01$). These consistently high ρ values showed that similarities in abundance data between stations were very strongly correlated to similarity in depths between stations and, therefore, assemblages changed continuously along vertical gradients.

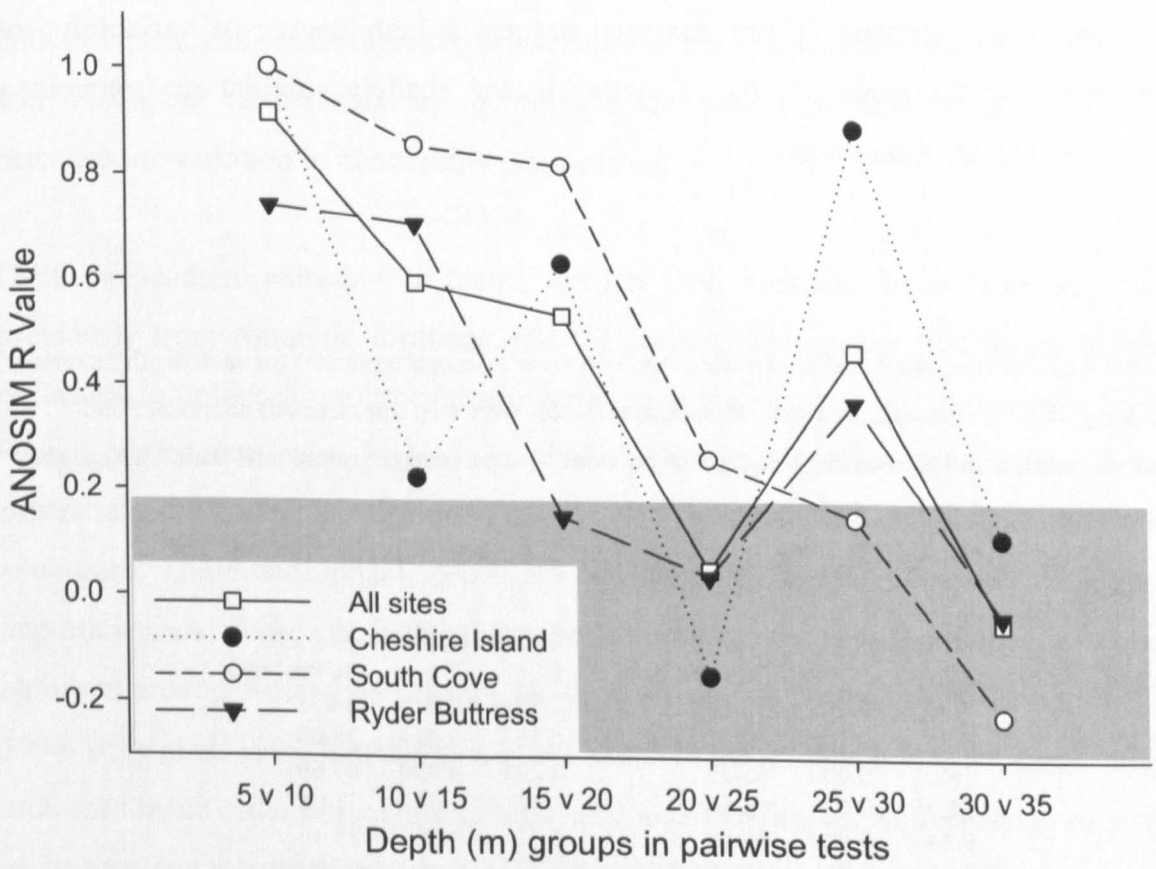


Figure 3.5 ANOSIM R values of pairwise tests of adjacent depth stations within each study (one-way tests, 10 permutations) and overall (two-way; site and depth factors 999 permutations). An ANOSIM R value of 1 indicates that depth groups were entirely dissimilar. Data points that lie within the grey box were not significant at the 10% level (P>0.1).

Patchiness

Nested ANOVA of both abundance and species richness data from stations at the same depth showed significant differences between replicate transects at 6 of the 7 depth increments sampled (Table 3.2). Furthermore, at two depth stations (15 and 20 m) the variation in abundance data between transects accounted for over 50% of the total observed variability (Table 3.2). As mentioned above, significant differences in faunal abundance between transects were also detected in the global (all depth stations) ANOVA, whilst MDS ordination showed that samples from replicate depth stations in the shallows were variable and as dissimilar to each other as they were to adjacent depth stations. These analyses suggest a high degree of variability and patchiness at the scale of 10s of meters in the shallow subtidal environment at Adelaide Island, Antarctica.

Table 3.2. Modified results table of nested ANOVA (site/ transect/ replicate) for each depth increment, showing variation between transects. Response variables were (log transformed) abundance and species richness and tests used 71 degrees of freedom. The percentages of the total variation (i.e. site, transect and error) derived from 'between transect' comparisons are also shown.

	Abundance			**Species richness**		
Depth	**F**	**P**	**% variance**	**F**	**P**	**% variance**
5	3.90	0.002	10.83	2.78	0.018	6.07
10	1.83	0.108	5.79	6.16	0.000	38.09
15	16.11	0.000	65.38	8.294	0.000	47.69
20	14.95	0.000	63.56	3.32	0.007	21.86
25	9.34	0.000	46.51	4.57	0.001	25.46
30	4.31	0.001	21.56	1.77	0.119	6.12
35	8.67	0.000	48.96	7.82	0.000	46.02

DISCUSSION

Changes in community structure with depth

The benthic assemblages at Adelaide Island changed significantly along a bathymetric gradient of 5 m to 35 m; the first hypothesis can therefore be accepted. Furthermore, communities at each site were highly distinct, despite the sites being separated by distances of only ~0.5, 3.5 and 4.0 km and having similar substrata types, slope aspects (i.e. southward facing) and current flows. The importance of local environmental conditions on structuring polar benthos has been previously suggested (Barnes 1995c, Ragua-Gil et al. 2004), and it seems likely that small-scale differences in the frequency of ice disturbance or variation in the gradient of the slope, combined with biological factors such as recruitment and predation, have resulted in high between-site variation in community composition.

Depth dependent patterns in faunal density and richness have been reported previously from Antarctic locations, but the current study is the first to use a fully replicated sampling design to evaluate variation at the site, transect and sample level. Faunal abundance was highest in the shallowest depth stations due to the superabundant gastropod mollusc *Nacella concinna* and the echinoid *Sterechinus neumayeri*. These widespread species are considered to be of considerable ecological importance, and dense grazing aggregations of both species at <10 m depth have been observed around Antarctica (Picken 1980, Kirkwood & Burton 1988, Brethes et al. 1994, Brey et al. 1995, Brockington et al. 2001). In the current study, species richness increased by an order of magnitude between 5 and 35 m depth. An increasing richness of fauna along a bathymetric gradient in the shallow subtidal zone has been reported previously at Signy Island in the South Orkney Islands (Barnes 1995c), King George Island in the South Shetland Islands (Jazdzewski et al. 1986, Nonato et al. 2000), Terra Nova Bay (Gambi et al. 2000), the Palmer Archipelago (Zamorano 1983) and McMurdo Sound (Dayton et al. 1970). At Adelaide Island, the speciose groups of sponges and bryozoans were not detected at depths less than 20 m, whilst at 30 and 35 m depth stations they were important contributors to richness. Sahade et al (1998) also recorded high species richness at 30 m depth at King George Island, although communities were dominated by ascidians rather than the structural sponges and bryozoans recorded at Adelaide Island.

The data suggested that the physical forces acting on assemblages at 5 m depth differed from those acting at 35 m depth. At the shallowest depth stations of all transects large sessile fauna were absent (although encrusting fauna probably existed on the underside of cobbles and were not detected by this sampling method), variation between transects was highest and the dissimilarity between adjacent depth stations was greatest. These observations strongly suggest that the physical disruptive force of ice is prominent at these depths, and that intense, discrete disturbance events result in patchy and dynamic communities dominated by errant organisms. Anchor ice (Dayton et al. 1970), ice scouring (Gambi et al. 2000, Nonato et al. 2000, Barnes & Brockington 2003) and the formation of winter fast ice (Barnes 1995b) can all result in a near denudation of sessile forms and low species richness in Antarctic shallows. At Adelaide Island, anchor ice formation is very rare but disturbance from iceberg scouring and the winter ice foot is both intense and frequent, particularly at 0-10 m depth (Brown et al. 2004, Smale et al. 2007a). It seems the constant scraping and encapsulation of substrata down to 10 m depth prohibits the growth of large sessile fauna in all but the most sheltered and protected refugia (but see Waller et al. 2006).

In conjunction with disturbance, the effects of large scale grazing at shallow depths may also drive the observed species distributions. Bowden (2006) reported strong effects of grazing, particularly by *Sterechinus neumayeri* at 8 m depth, on artificial hard substrata, which he suggested considerably restricted the recruitment and development of sessile fauna. High densities of limpets and sea urchins were recorded at the shallowest depth stations, and intense grazing by these species may inhibit the settlement and growth of sessile recruits originating from deeper water.

With increasing depth, adjacent depth stations generally became more similar, and variation between transects at each site decreased, as demonstrated by MDS ordinations and ANOSIM R values. It seems that biological factors such as competition, predation, recruitment and development had more influence on assemblage composition as depth increased. Dayton et al. (1974) described the benthos at 33-60 m depth at McMurdo Sound as being dominated by a diverse group of structural sponges, competing primarily for space, and being regulated by asteroid and molluscan predators. Intense competition for space at depths greater than 30 m

has also been reported at lower latitude Antarctic locations (Barnes 1995c). At Adelaide Island, it seems that a decreasing frequency of disturbance with depth may have resulted in communities at >30 m depth being more homogenous and characterised by structural sessile fauna, which in turn may have promoted species richness by increasing habitat complexity and providing space for epifauna (Dayton et al. 1974, Gutt & Schickan 1998). Interestingly, sessile forms dominated at shallower depths and species richness was higher at Ryder Buttress compared with Cheshire Island and South Cove. This site had the steepest sloped topography, which included overhangs and crevices, and as a result may be more protected from ice disturbance. As a result of decreased disturbance pressure, complex sessile assemblages may have developed at shallower depths at Ryder Buttress, although at this stage the hypothesis that the observations were purely due to a 'site effect', rather than increased protection from ice scouring cannot be rejected.

Patchy distributions along a continuum

Examples of species being distributed along an environmental gradient are plentiful in nature, with perhaps the most well known being the distribution of vegetation along an altitudinal cline (e.g. Beals 1969, Hemp 2006) and the position of intertidal organisms on a rocky shore (Colman 1933, Stephenson & Stephenson 1972). Early studies of the distributions of biota on the intertidal rocky shore led to the paradigm of 'zonation'; the idea that communities were arranged in vertical bands or zones, perhaps as a result of physical constraints, reproductive potential, competition or grazing pressures (see Underwood 1991 and references therein). However, communities are not distributed in discrete zones with defined boundaries but are patchily distributed along environmental gradients, and the notion of zonation rather oversimplifies a highly variable system (Underwood 1978, Underwood & Chapman 1995, Benedetti-Cecchi 2001). Despite a widespread acceptance in temperate and tropical marine ecology that intertidal zonation is an over-simplification, the concept of marine communities being distributed in zones has re-emerged in polar ecology (Gambi et al. 1994, Sahade et al. 1998, Barnes & Brockington 2003).

To expand, some researchers have described three zones of benthos in Antarctic shallow waters; a zone from 0 to ~15 m depth dominated by errant grazers and scavengers, principally *Nacella concinna*, *Sterechinus neumayeri* and *Odontaster*

validus; a zone from ~15 m to ~30 m depth comprising primarily of suspension feeders such as polychaetes, holothurians and cnidarians; and a zone below ~30 m depth dominated by large sessile taxa such as sponges and ascidians (Dayton et al. 1970, Sahade et al. 1998). Similarly to the early observations made in the rocky intertidal, these 'zones' are simply areas where some of the more conspicuous species have optimal distributions, but the 'zones' in effect do not support distinct assemblages. For example, representative images from one of our study sites, Cheshire Island (Fig. 3.6), show that at a glance, limpets seem to characterise the shallows (5 m depth), anemones are conspicuous at ~20 m depth and sponges dominate at 35 m depth. However, these observations simply reflect the optimal distributions of highly conspicuous species, and not communities as a whole. Therefore, the second hypothesis, predicting that assemblages change along a continuum must be accepted, as multivariate analysis of assemblage composition shows no evidence of groupings into defined zones. In fact, communities at Adelaide Island (and probably elsewhere) change continuously from 0 m to 35 m depth, with adjacent depth increments becoming more similar with increasing depth. Discrete zones or bands are not present at any depth.

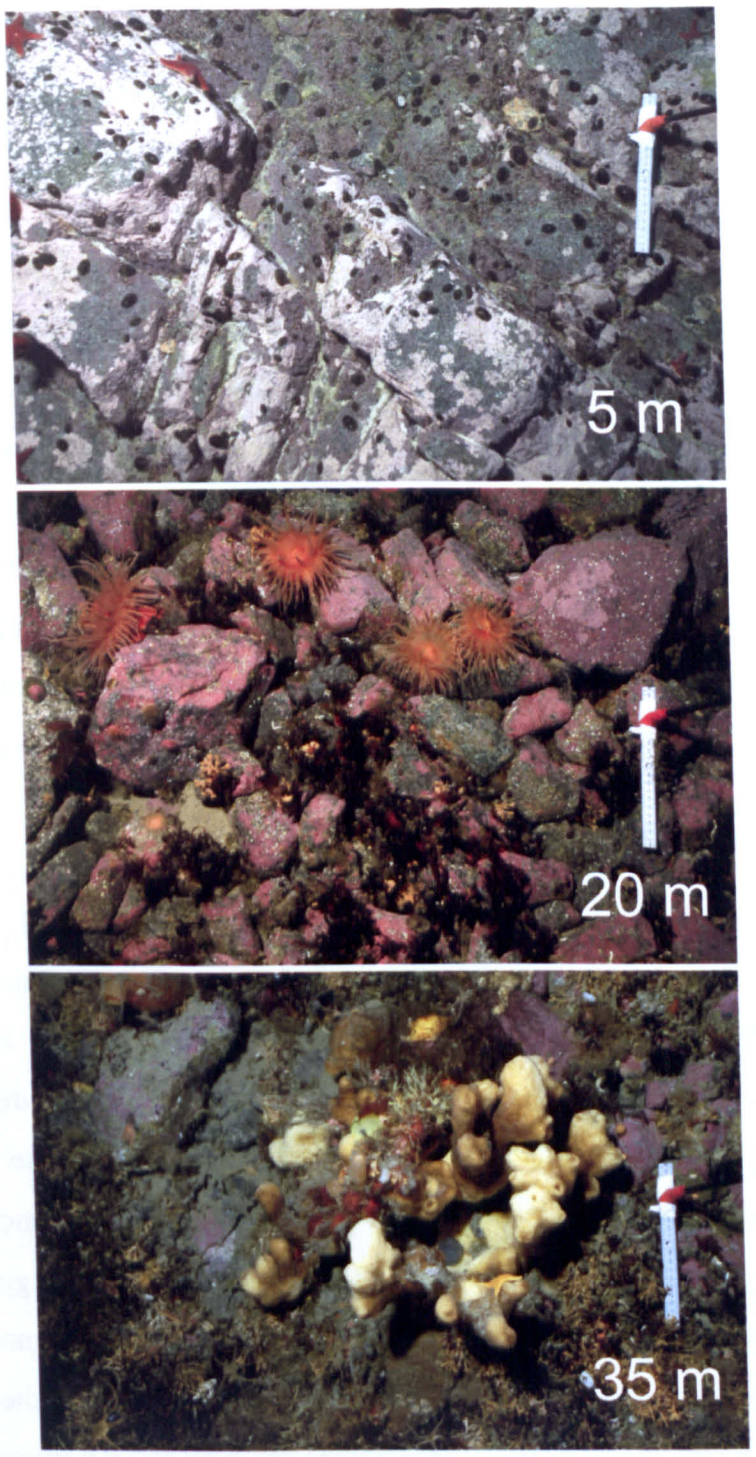


Figure 3.6 Representative examples of photoquadrats collected at 5, 20 and 35 m depth at the Cheshire Is. study site (Adelaide Is., Antarctica). Images show conspicuous fauna that dominate each depth increment; the limpet *Nacella concinna* at 5 m depth; various anemones and holothurians at 20 m depth; and large sponges and bryozoans at 35 m depth.

The concept of zonation in polar subtidal communities oversimplifies a highly variable and patchy environment. In the current study, significant differences between stations at the same depth just 10 m apart were observed, whilst variation at the scale of 1 m (between replicate) was also high. Therefore the hypothesis (3) that horizontal patchiness across the bathymetric gradient is significant can be accepted. The distribution of species in Antarctic shallow waters is inevitably highly heterogeneous as it is widely accepted as being driven (to some degree) by the physical pressures of ice disturbance. Iceberg scouring, by its very nature, is highly stochastic in space and time (Brown et al. 2004) and these discrete disturbance events create of patchy mosaic of assemblages at differing stages of recovery in polar waters (Gutt & Piepenburg 2003, Conlan & Kvitek 2005). To suggest that species are distributed in zones or depth bands ignores the small-scale patchiness and habitat heterogeneity that, at larger scales, may promote high levels of biodiversity in the shallow regions of the Antarctic shelf (Gutt & Piepenburg 2003).

Communities at Adelaide Island were generally both rich and abundant, but community structure varied significantly with depth and site. This variability is perhaps driven by the intensity of ice disturbance, although there is currently no empirical data to suggest that disturbance intensity varies between depths and sites (see Chapter 6). Intuitively, the lack of sessile fauna inhibiting the exposed hard surfaces in the shallows (<10 m depth) suggested that the frequency of physical disturbance is high in the very shallow subtidal zone. The data suggests, to some degree, that benthic assemblages are distributed along a disturbance gradient in nearshore polar habitats such as Adelaide Island, but why? What are the direct effects of a disturbance event and over what time scales are benthic communities affected? These questions form the basis of Chapters 4 and 5.

Chapter 4 – The catastrophic nature of iceberg scouring

The data in this chapter are also published as: Smale D. A., Barnes, D. K. A. and Fraser, K. P. P. (2007) The influence of ice scour on benthic communities at three contrasting sites at Adelaide Island, Antarctica. Austral Ecology 32: 878-888.

Chapter 4 – The catastrophic nature of iceberg scouring

INTRODUCTION

The grounding out of icebergs on the seabed is an intense natural disturbance, which can be catastrophic at small scales. It has been described as one of the five most significant disturbances acting on large ecosystems (Gutt & Starmans 2001) and may influence up to one fifth of the Earth's coastlines (Gutt 2001). Sonar examination of even mid-latitude temperate seas has revealed criss-crosses of old ice scours from the last ice age (Barrie et al. 1992, Duncan & Goff 2001). Grounded icebergs can alter physical seabed characteristics, such as sediment type, current flow and topography (Lien et al. 1989), whilst destroying benthos (Gutt et al. 1996, Peck et al. 1999, Gerdes et al. 2003, Conlan & Kvitek 2005). In the Antarctic, the ecological effects of ice scouring have been comprehensively studied in deeper waters of the Weddell Sea (Gerdes et al. 2003, Gutt & Piepenburg 2003, Teixido et al. 2004), whilst there have been far fewer studies involving scours in nearshore waters (Lenihan & Oliver 1995, Peck et al. 1999, Lee et al. 2001). However, the effects of shallow water ice-scouring and the subsequent recolonisation processes in the Canadian Arctic have been well described (Conlan et al. 1998, Conlan & Kvitek 2005). It has been suggested that ice scouring promotes biodiversity at larger scales by increasing habitat heterogeneity (Gutt & Piepenburg 2003), removing dominant competitors (Barnes 2002) and providing opportunities for a diverse group of scavengers (Presler 1986, Arntz et al. 1994, Gerdes et al. 2003). Thus, ice disturbance may be a key factor in explaining high benthic diversity on the Antarctic continental shelf.

The effects of ice scouring are not limited to polar shores; sea ice disturbance may also structure mid-latitude nearshore communities (Keats et al. 1985, McCook & Chapman 1993, Minchinton et al. 1997). Despite the widespread occurrence of ice scouring, few data exist concerning the immediate destruction of benthos and early successional processes. In fact, only two Antarctic iceberg scours of known age have been sampled within days of formation (Peck et al. 1999) whilst most studies involve older scours that have been crudely aged retrospectively following estimation of community growth rates and the physical degradation of the scour mark (Gutt &

Starmans 2001, Gutt & Piepenburg 2003). In soft sediments Peck et al. (1999) recorded a 99.5% reduction in macrofaunal abundance, whilst on shallow hard substrata communities may be held at early successional stages due to a continuous scraping and knocking by ice (McCook & Chapman 1993, Barnes 1995c, Pugh & Davenport 1997).

Even at local scales, variation in the frequency of ice scour has a significant effect on the benthos, with age, size and taxa distributions all linked to scouring regimes (Brown et al. 2004). Heavily impacted locations often support communities characteristic of a high disturbance regime, typically exhibiting low diversity, percentage cover and biomass and a high abundance of pioneers (McCook & Chapman 1993, Barnes 1995c, Brown et al. 2004).

Assemblages in twelve recently formed scours were compared with nearby undisturbed benthos in the shallows of Adelaide Island. Scours at three contrasting sites were studied in order to elucidate the influence of site exposure, sediment size and substratum type on the effects of iceberg impacts.

METHODS

Study sites

Iceberg scours were studied at Hangar Cove, South Cove and Lagoon Bay. These sites were selected as icebergs are frequently seen grounded at each site, but the substratum type and benthic assemblages are thought to differ between sites. Lagoon Bay is a cove on the southwest of Lagoon Island, a small outcrop ~4 km southwest of Rothera Point. The slope at Lagoon Bay is similar to that at the other two study sites and a preliminary survey showed some evidence of iceberg scouring at depths of 5-20 m. Prior to this study, there have been no detailed descriptions of the benthic assemblages at this site.

Sampling protocol

Twelve iceberg scours created during the austral summers of 2004/05 and 2005/06 were selected for sampling. Travelling icebergs that were likely to impact the selected sites were monitored and their positions fixed with GPS once grounded. Following iceberg 'retreat' from newly created scours, SCUBA divers sampled both the

disturbed benthos and the assemblages in the adjacent undisturbed zone. Fresh scours were sampled as soon as practically possible, with the maximum time lag being 20 days (due to weather and ice conditions) and the minimum being one day after the iceberg grounding. All the icebergs that created the study scours were of a similar size (ca. 3-5 m height above sea level and about 10-30 m long), grounded at similar depths (10-17 m) and remained grounded for no more than 48 hours. Four scours from each of the three study sites were selected for study.

For all twelve scour events, three random samples of replicate 0.03 m^2 areas were taken from both the scoured area and an adjacent undisturbed area. Scour samples were taken from the trough zone of the scour; berms were not sampled as they were often too small or poorly formed. Undisturbed samples were collected from an area (with no signs of previous scour marks) about 5 m away from each scour, at an equivalent depth. At the sites consisting primarily of boulders and cobbles (South Cove) or a thin layer of silt (Lagoon Bay), samples were obtained by hand clearing 3 replicate 0.03 m^2 randomly placed quadrats. The substratum at Hangar Cove was too thin and variable to core effectively and hand-clearing quadrats proved impractical, so a scoop and mesh bag sampler was developed. This was used to sample a 0.03 m^2 area of sediment to a depth of 2 cm. All samples were sieved through a 0.5 mm mesh (fauna retained on this mesh size hereon defined as 'macrofauna'), coarsely sorted and preserved in 70% ethanol for subsequent taxonomic analysis. Wet weight for all fauna was obtained for biomass analysis.

Physical characteristics

SCUBA divers also measured the length and width of each scour. To assess the substrata characteristics, 3 cores (30 mm diameter, 100 mm depth) were collected from an undisturbed area at each site for analysis of sediment size distribution. Cores were later sieved and particle size fractions were quantified by the Wentworth scale (Wentworth 1922). To evaluate the major substratum types at each site (i.e. larger particle size fractions), the percentage surface cover of bedrock, boulders, cobbles, pebbles and fines from ten random 0.25 m^2 quadrats was estimated (substratum sizes defined by Wentworth (1922)).

Statistical analysis

Site means were obtained by pooling the three replicates and averaging across the four scour events. All means are presented ± standard error. Sample abundance, richness and biomass data required a log transformation to reduce heterogeneity. Variation between scours and undisturbed areas ('disturbance' factor) was analysed with a mixed model ANOVA in Minitab 14.0. Scour events (i.e. paired sample sets from scours and undisturbed areas, 'event' factor) were nested within site, which was treated as a random factor. Furthermore, each species sampled was designated a primary or secondary consumer based on its general feeding style. The percentage abundance of each trophic group was calculated, arc-sine transformed and differences between scours and undisturbed areas were tested using the mixed model ANOVA. Differences within a site were examined with *t* tests and *P* values of < 0.05 were considered significant in all tests. Multivariate analyses were applied using PRIMER Version 6 (Clarke 1993, Clarke & Warwick 2001). A similarity matrix of all samples was produced using a Bray-Curtis index following a square root transformation of abundance data. The relatedness of scoured and unscoured communities was assessed using multidimensional scaling (MDS) ordination. A SIMPER analysis was used to determine which taxa contributed most to the observed dissimilarity between scour and undisturbed samples.

RESULTS

Physical characteristics

Each newly formed scour had a distinctive trough zone, which contrasted with an adjacent undisturbed area. A typical scour (although older and not a study scour) with the clearly defined sampling zones is presented in figure 4.1. The maximum depth of the iceberg keel incision was estimated at 0.1-0.2 m below the surrounding substratum. The length of the study scours ranged from 1.3 m to 5.8 m, with a mean length of 3.2 ± 0.4 m. Scour morphology was generally elongated, with a mean width: length ratio of 1: 2.7 ± 0.5 (Table 4.1).

The three study sites varied in substratum type. Hangar Cove was primarily a soft sediment habitat (68.0 ± 4.3% seabed cover of fines) whilst South Cove consisted of

semi-stable substrata (39.0 ± 5.9% cobbles, 30.5 ± 3.8% pebbles). Lagoon Bay was an intermediate between the other two sites (Table 4.2a). The smaller particle size fractions also differed between the sites. The sediment at Hangar Cove and Lagoon Bay consisted of silt and very fine sand (47.4% and 57.3% total mass), whilst the South Cove sediment was dominated by fine/ medium sand (69.3%, Table 4.2b).

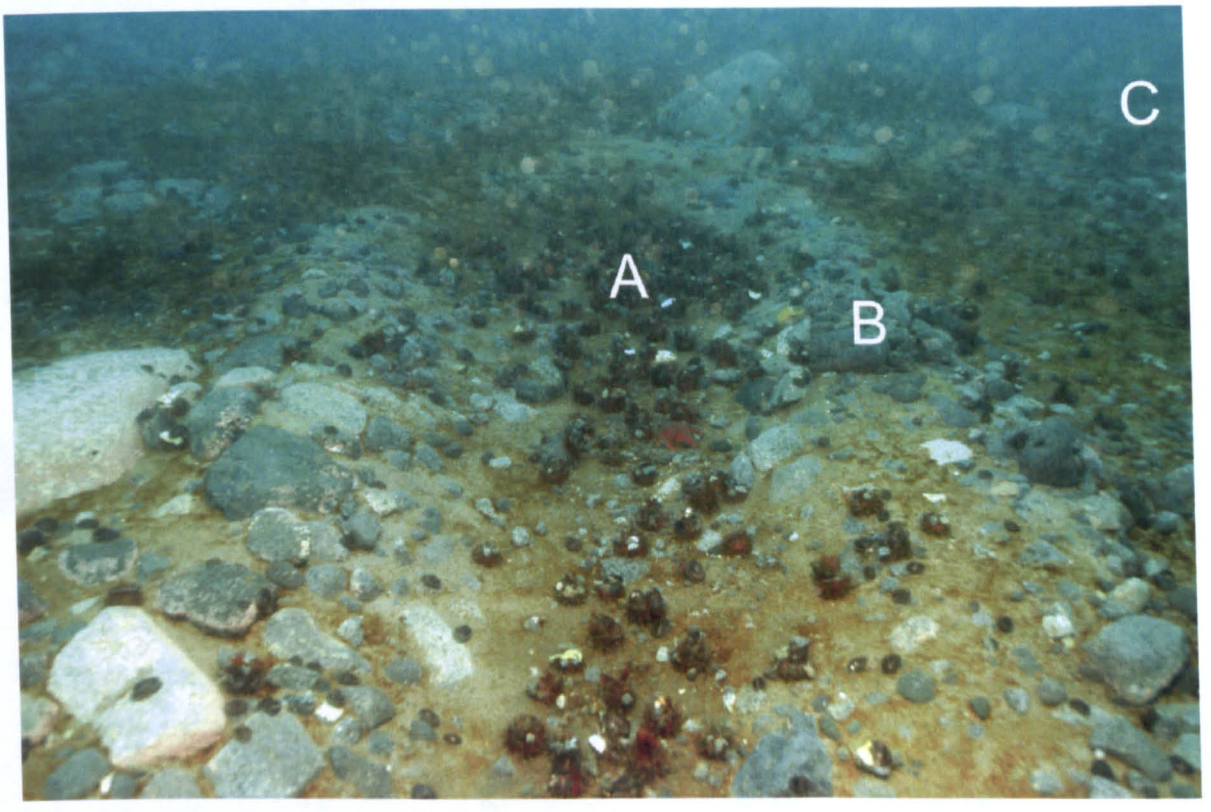


Figure 4.1 A representative iceberg scour at ~15 m depth at South Cove. This scour was older than the scours sampled for the study, and dense aggregations of scavenging macrofauna have formed in the trough zone. Three distinct zones can be identified; the disturbed trough zone (A), the raised berm (B) and an adjacent area, which remains relatively undisturbed (C).

Table 4.1 Locations, dimensions, depths and formation dates of all study scours at Adelaide Is., WAP. Scour width is given as the mean of 3 in *situ* measurements. All icebergs were grounded for less than 48 hours and sampling lag is the time delay between the iceberg impact and the benthic sampling.

Site-Scour	Length (m)	Width (m)	Depth (m)	Impact date	Sampling lag
Hangar-1	3.1	1.8	14	23.03.2004	13 days
Hangar-2	2.8	1.1	13	15.06.2004	18 days
Hangar-3	5.8	1.1	15	01.07.2004	20 days
Hangar-4	1.3	0.3	12	06.02.2006	8 days
South-1	3.1	2.7	17	05.06.2004	4 days
South-2	2.6	1.0	10	28.02.2005	1 day
South-3	4.5	2.8	17	27.04.2005	4 days
South-4	2.5	1.0	16	08.02.2006	6 days
Lagoon-1	3.0	0.4	13	19.01.2006	9 days
Lagoon-2	2.0	0.9	14	20.01.2006	10 days
Lagoon-3	5.5	2.6	16	24.01.2006	14days
Lagoon-4	2.5	1.6	14	25.01.2006	15 days

Table 4.2a Percentage cover of large particle size fractions (Wentworth Scale) at each study site at Adelaide Is., WAP. Data are mean surface area coverage of 10 replicate 0.25 m^{-2} quadrats placed randomly across disturbed and undisturbed zones at ~12m depth (± SE).

Substrata	Size	Hangar Cove	South Cove	Lagoon Bay
Boulders	>256 mm	2.0 ± 2.0	7.5 ± 2.7	0.0 ± 0
Cobbles	64-256 mm	5.0 ± 2.2	39.0 ± 5.9	7.5 ± 2.5
Pebbles	4-32 mm	25.0 ± 3.3	30.5 ± 3.8	34.0 ± 5.4
Fines	>4 mm	68.0±4.3	23.0 ± 4.8	58.5 ± 6.3

Table 4.2b Mean percentage (n = 3 cores) of total mass of small particle fractions (± SE). Size fractions taken from Wentworth scale and cores randomly collected at ~12m depth.

Particle	Size	Hangar Cove	South Cove	Lagoon Bay
Gravel	>2 mm	17.7 ± 2.8	14.0 ± 1.6	20.0 ± 1.2
Very coarse sand	1-2 mm	2.3 ± 0.4	5.0 ± 2.1	1.1 ± 0.2
Coarse sand	0.5-1 mm	3.1 ± 0.4	8.6 ± 3.0	1.7 ± 0.1
Medium sand	250-500 μm	6.5 ± 1.1	31.1 ± 1.8	3.3 ± 0.4
Fine sand	125-250 μm	23.4 ± 8.0	38.2 ± 3.0	16.7 ± 3.7
Very fine sand	63-125 μm	29.5 ± 8.4	3.1 ± 0.1	40.9 ± 2.5
Silt/ Clay	<63 μm	17.9 ± 3.1	0.0 ± 0.0	16.4 ± 1.2

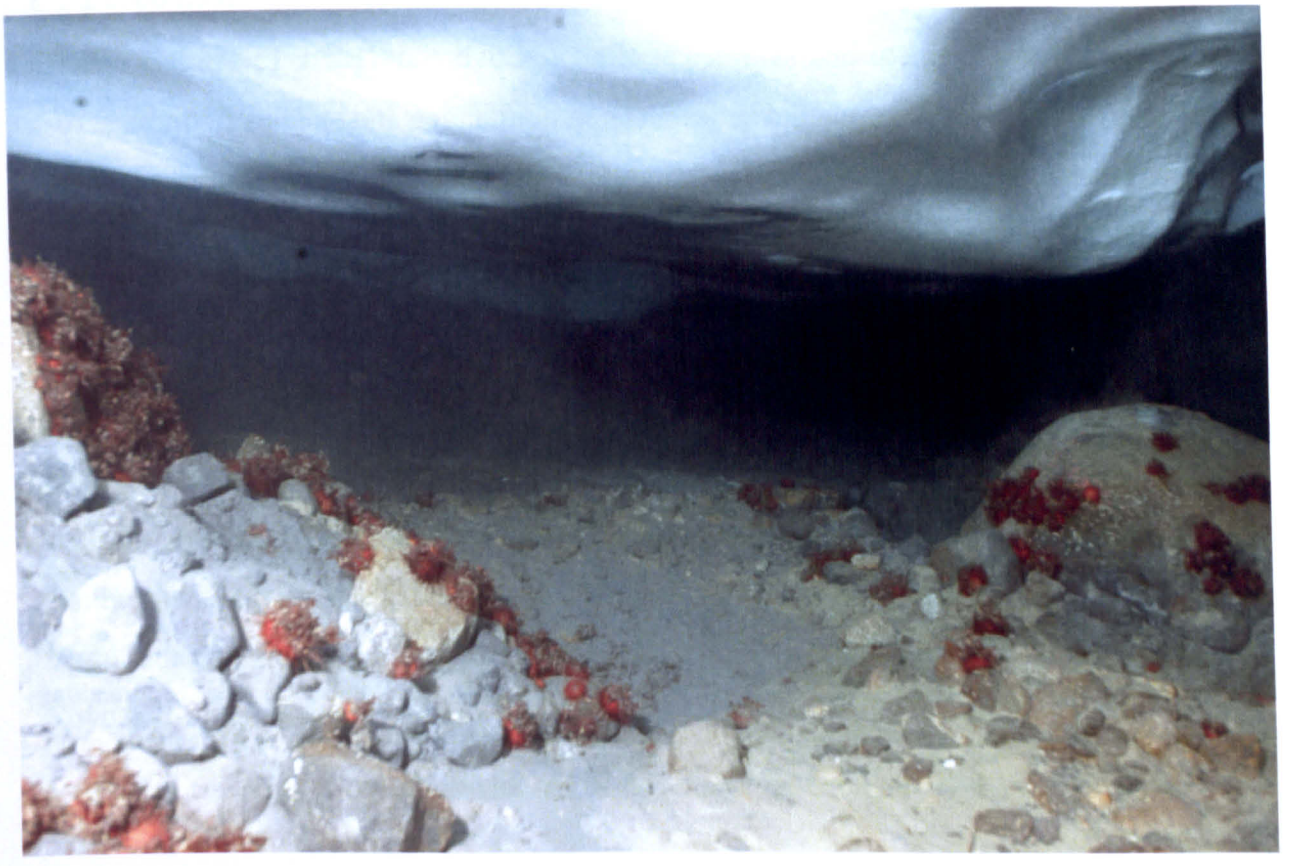


Figure 4.2 A newly formed scour at ~12 m depth at Hangar Cove. The image was taken during winter whilst the iceberg was 'locked-in' by seasonal fast ice and therefore impacted the seabed at each low tide. Dense aggregations of the regular echinoid *Sterechinus neumayeri* quickly formed on the raised berms and within the scour trough zone at Hangar Cove, which often resulted in higher biomass values in disturbed samples compared with undisturbed samples.

Comparisons of scoured and undisturbed assemblages

Overall, scour assemblages had significantly lower abundance and richness values than undisturbed assemblages (Table 4.3). There was also a significant interaction between site and disturbance when analysing species richness and biomass, due to a smaller difference between scours and undisturbed samples at Hangar Cove compared with South Cove and Lagoon Bay (Table 4.3, Fig. 4.3). The maximum difference in abundance was recorded at Lagoon Bay, where fauna were 97.8 ± 0.8% less abundant in scours compared with undisturbed areas. Faunal abundances in scours at the Hangar Cove and South Cove sites were 95.1 ± 1.2% and 91.8 ± 6.3% lower than undisturbed areas, respectively (Fig. 4.3). The greatest difference in species richness

was also observed at Lagoon Bay, where scour assemblages were 83.7 ± 6.1% less speciose than undisturbed assemblages. Similarly, scour samples contained 60% ± 2.3 less species than undisturbed samples at Hangar Cove and 81.2 ± 13.1% less species at South Cove (Fig. 4.3). Unlike differences in abundance and species richness across sites, patterns of biomass varied considerably with site, and overall biomass was not significantly different between scours and undisturbed areas (Table 4.3). There was no difference in mean biomass between scours and undisturbed areas at Hangar Cove, primarily due to the presence of large echinoids, *Sterechinus neumayeri*, in the newly formed scours. Aggregations of this echinoid rapidly formed in fresh scours at this site and densities may be higher in disturbed areas than in undisturbed sediments (fig. 4.4).

Table 4.3. Results of mixed model ANOVA with scour events nested within sites, sites as a random factor and disturbance (i.e. scour vs. undisturbed) fixed. The response variables are log transformed faunal abundance, species richness and total biomass. An asterisk denotes a significant result ($P < 0.05$).

Mixed Model ANOVA: Log abundance

Source	DF	SS	MS	F	P
site	2	15.602	7.801		
event(site)	9	19.527	2.170	1.83	0.190
disturbance	1	206.424	206.424	152.45	0.006*
site*disturbance	2	2.708	1.354	1.14	0.361
disturbance*event(site)	9	10.651	1.183		
Error	48	16.190	0.337		
Total	71	271.103			

Mixed Model ANOVA: Log species richness

Source	DF	SS	MS	F	P
site	**2**	**0.2299**	**0.1149**		
event(site)	9	5.9365	0.6596	2.06	0.148
disturbance	1	35.0108	35.0108	24.44	0.039*
site*disturbance	2	2.8653	1.4326	4.48	0.045*
disturbance*event(site)	9	2.8794	0.3199		
Error	48	5.3255	0.1109		
Total	71	52.2474			

Mixed Model ANOVA: Log biomass

Source	DF	SS	MS	F	P
site	2	50.089	25.045		
event(site)	9	58.203	6.467	1.86	0.184
disturbance	1	157.401	157.401	8.99	0.096
site*disturbance	2	35.028	17.514	5.04	0.034*
disturbance*event(site)	9	31.268	3.474		
Error	48	116.824	2.434		
Total	71	448.815			

The scour assemblages were generally poor in terms of both abundance and species richness. Mean faunal abundance of the scoured community was 21.3 ± 5.3 inds.0.09 m^{-2} at Hangar Cove, 10.3 ± 6.6 inds.0.09 m^{-2} at South Cove and 7.8 ± 3.6 inds.0.09 m^{-2} at Lagoon Bay. The mean number of species in each scour sample was 7.2 ± 0.5, 4.8 ± 1.4 and 4.9 ± 1.9 at Hangar Cove, South Cove and Lagoon Bay respectively. The least abundant and most depauperate assemblage was found in the 'LAG3' scour at Lagoon Bay. Only seven individuals and 4 taxa were present in the 0.09 m^2 sampling area. In contrast, 556 individuals representing 31 taxa were sampled in the unscoured benthos just a few metres away. Abundance between scours varied by an order of magnitude, ranging from 10-119 individuals to 7-65 individuals per 0.09 m^{-2} at South Cove and Lagoon Bay respectively.

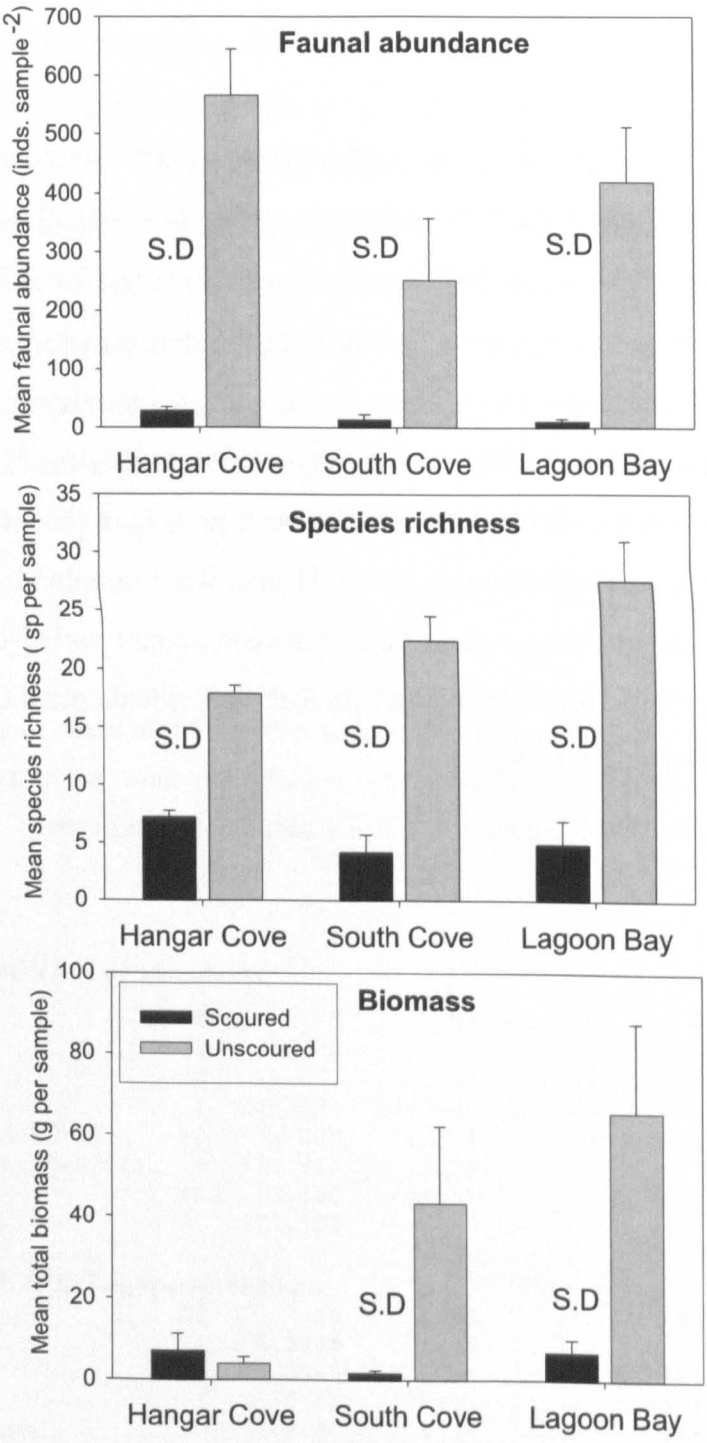
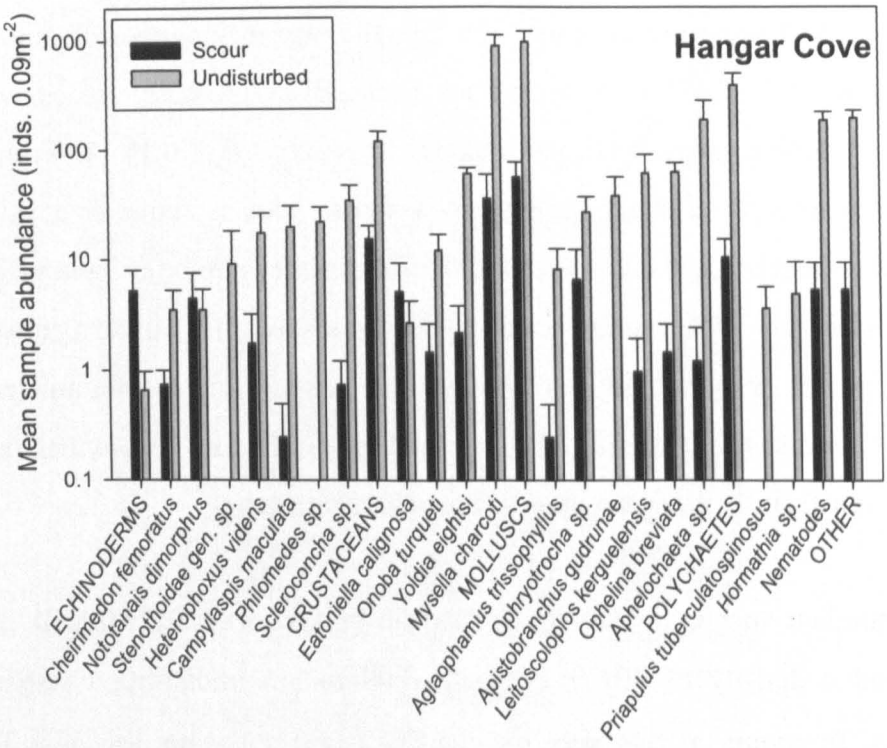


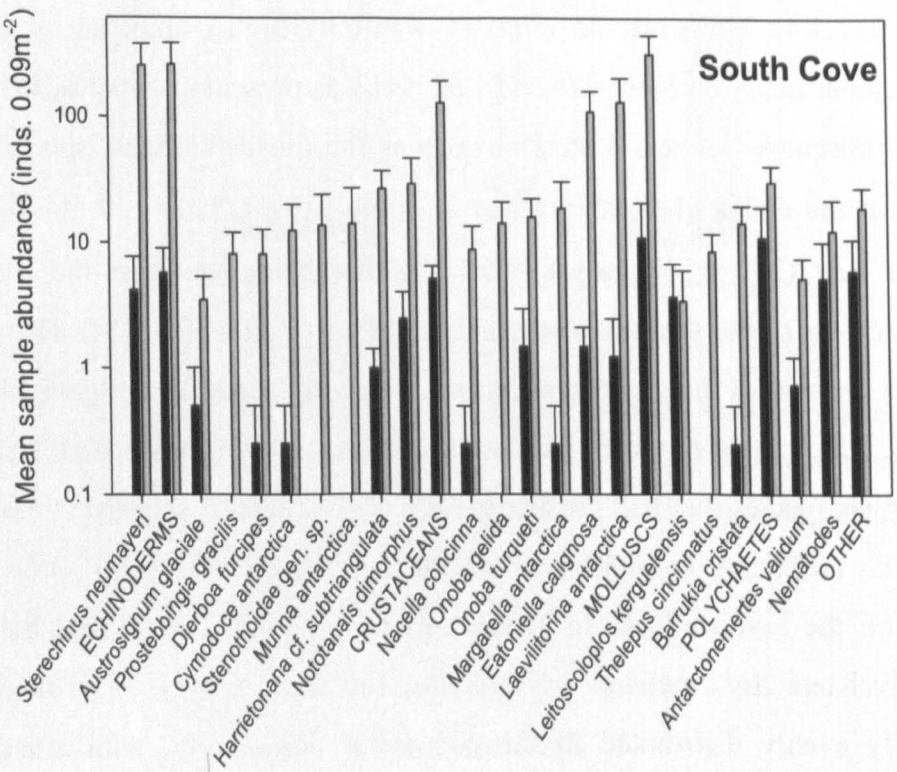
Figure 4.3 Abundance, species richness and biomass of scoured (black bars) and unscoured assemblages (grey bars) at Hangar Cove, South Cove and Lagoon Bay, Adelaide Island, Antarctica. Data are shown as mean across all four scours within each site (± SE). 'S.D' denotes significant difference between scoured and unscoured assemblage ($P < 0.05$).

Ideally, each scour would have been sampled immediately after formation but this was not possible. Therefore, it is important to assess the influence of the lag time in sampling on the results. It is clear from Table 1 that the study scours at South Cove were sampled sooner after formation than the scours at the other sites, seemingly confounding any inter-site comparisons. However, examination of the residuals and a linear regression of sampling lag time with faunal abundance suggested there was no relationship ($R^2 < 0.05$, $P > 0.1$). Species richness or biomass values were also unrelated to sampling delay (both parameters: $R^2 < 0.05$, $P > 0.1$). A further factor inhibiting comparisons of scour communities across sites is scour size. All scours were elongated trenches and a crude estimate of scour area can be calculated by scour length multiplied by mean scour width. Regressions of this value against faunal abundance, species richness and biomass show no relationship (all parameters: $R^2 < 0.05$, $P > 0.1$) and suggest that (at this scale and stage of scour recolonisation) scour size did not significantly influence assemblage characteristics.

The most abundant species in the study was the bivalve mollusc *Mysella charcoti*, which reached a density of 891 ± 226 inds.0.09 m^{-2} in undisturbed sediments at Hangar Cove. In scours at this site, the density of *M. charcoti* was just 36 ± 24 inds.0.09 m^{-2}; the largest difference between scours and undisturbed areas recorded in the study (Fig. 4.4). However, *M. charcoti* was only highly abundant at one site, whilst the regular echinoid *Sterechinus neumayeri* was present at all sites, in both the scoured and unscoured zones. *S. neumayeri* was the most numerous species of the macrofauna in the undisturbed community at South Cove (251 ± 120 inds.0.09 m^{-2}) and Lagoon Bay (257 ± 57 inds.0.09 m^{-2}) whilst being amongst the five most abundant members of the scoured community at all three sites (Fig. 4.4). Densities of *S. neumayeri* underwent the greatest reduction following scouring at South Cove and Lagoon Bay, although its numbers increased in the scoured benthos of Hangar Cove (Fig. 4.4). Other species that had notably greater abundances in scoured communities compared with unscoured communities were the gastropod *Eatoniella calignosa* (at Hangar Cove), the bivalve mollusc *Yoldia eightsi* (at South Cove) and the errant nephtyid polychaete *Aglaophamus trissophyllus* (at South Cove). The major taxa were typically evenly distributed in the post-scour community, with crustaceans,

echinoderms, molluscs and polychaetes well represented (Fig. 4.4). At a coarse taxonomic level, the scour communities at Hangar Cove differed from those at the other sites as molluscs dominated faunal abundance (due to high numbers of *Mysella charcoti* in three of the scours) and echinoderms were more abundant in scours than undisturbed areas.





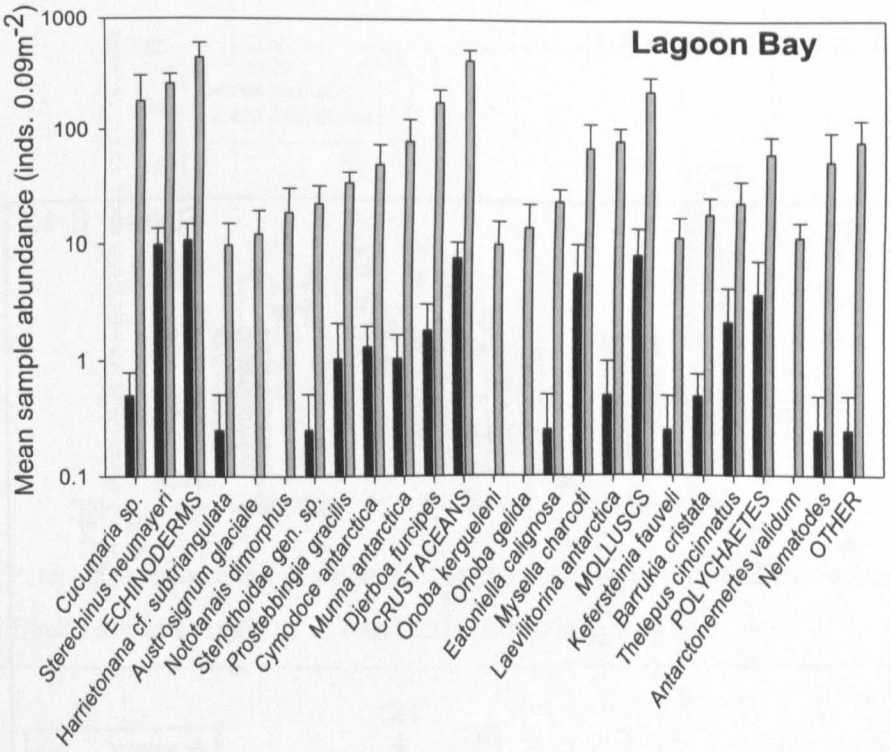


Figure 4.4 Mean abundance of taxa (± SE) in both scours (black bars) and undisturbed areas (grey bars) at all three study sites at Adelaide Island, Antarctica (n = 4 scours or undisturbed areas at each site). The 20 most abundant taxa at each site, and totals for coarse taxonomic groups where species can be aggregated (in upper case), are shown.

The MDS ordination of samples from all sites depicts a difference in community composition as a result of iceberg scouring, with scoured and unscoured assemblages distinctly grouped (Fig. 4.5). Furthermore, variability within the scour samples was much greater than in the undisturbed samples, which were closely grouped by site (Fig. 4.5). The results of the SIMPER analysis show that the taxa responsible for the observed difference between scour and undisturbed samples varied with site (Table 4.4). At Hangar Cove, just 3 species were responsible for 40% of the dissimilarity between sample groups, whilst at the other sites contributions were more evenly distributed over more taxa. The most abundant member of the undisturbed community (*Mysella charcoti* at Hangar Cove and *Sterechinus neumayeri* at South Cove and Lagoon Bay) was the biggest contributor to dissimilarity at all sites, perhaps due to its high density in undisturbed areas. The polychaete *Leitoscoloplos kerguelensis,* previously reported as being associated with disturbed sediments (see Barnes & Conlan 2007 and references therein), was more abundant in scours than undisturbed samples at Hangar Cove (Fig. 4.4). *L. kerguelensis* was the only major contributor to

the observed difference between groups to have a higher abundance in scours rather than undisturbed zones (Table 4.4).

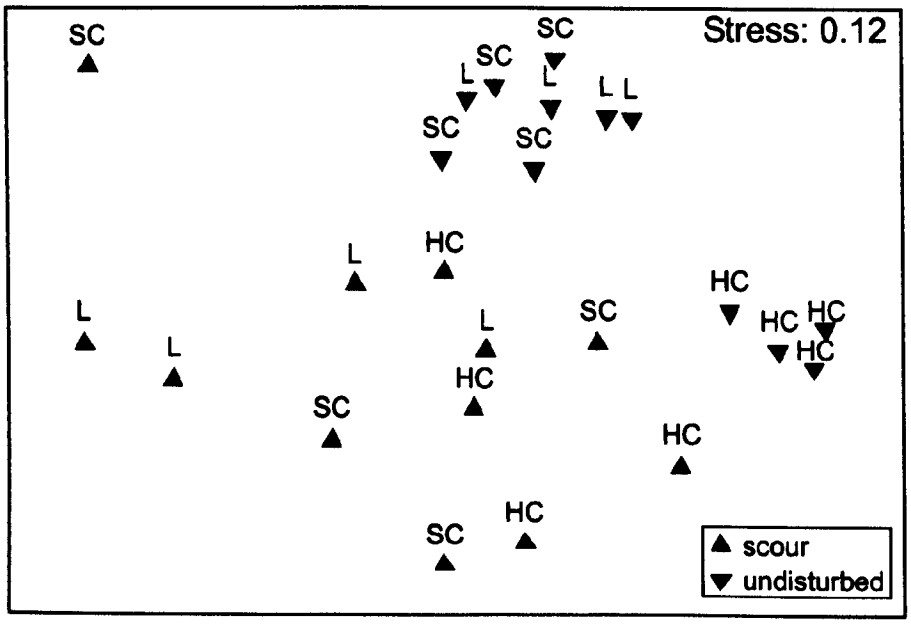


Figure 4.5 MDS plot generated from Bray-Curtis co-efficient matrix of faunal abundance (square root transformed) of scour and undisturbed areas at Hangar Cove (HC), South Cove (SC) and Lagoon Bay (L), Adelaide Island, Antarctica (three replicate samples pooled).

The ANOVA showed no significant difference in the percentage abundance of secondary consumers between scour and undisturbed areas. However, there was a suggestion of a disturbance and site interaction ($F = 3.61$, $P = 0.07$) and the mean percentage of secondary consumers in scours (compared with undisturbed samples) was high at Hangar Cove and low at Lagoon Bay (Fig. 4.6).

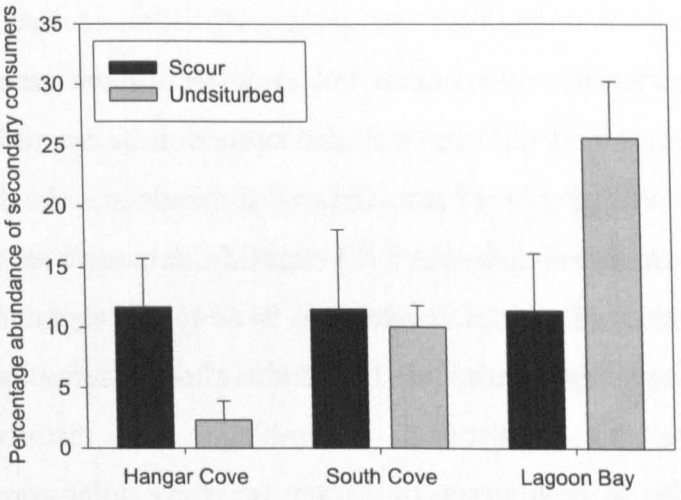


Figure 4.6 Percentage abundances of secondary consumers in scours and undisturbed areas at the three study sites. Data are means (± SE) of all four sample sets within each site.

Table 4.4. Taxa contributing to differences (50% cut-off) between scour and undisturbed samples, based on SIMPER analysis of square-root transformed data. Overall differences between groups are shown in parentheses.

Group	Taxa	%	Cum %
Hangar Cove: scour vs. undisturbed (78%)			
	Mysella charcoti	20	20
	Aphelochaeta sp.	10	30
	Nematodes	10	40
	Ophelina breviata	6	46
	Leitoscoloplos kerguelensis	5	51
South Cove: scour vs. undisturbed (83%)			
	Sterechinus neumayeri	13	13
	Laevilitorina antarctica	9	22
	Eatoniella calignosa	8	30
	Harrietonana cf. subtriangulata	4	34
	Barrukia cristata	4	38
	Onoba turqueti	3	41
	Nototanais dimorphus	3	44
	Margarella antarctica	3	47
	Onoba gelida	3	50
Lagoon Bay: scour vs. undisturbed (86%)			
	Sterechinus neumayeri	9	9
	Djerboa forcipes	8	17
	Laevilitorina antarctica	6	23
	Cucumaria sp.	6	29
	Munna antarctica.	6	35
	Cymodoce antarctica	4	39
	Nematodes	4	43
	Eatoniella calignosa	4	47
	Mysella charcoti	4	51

DISCUSSION

Iceberg scouring is frequently described as one of the most intense and frequent disturbances in the marine environment but its effects have rarely been directly measured. Peck et al. (1999) reported a 99.5% reduction in macrofaunal abundance from a coastal scour at Signy Is. (South Orkney archipelago). In the current study, known-age scours from locations inside the Antarctic Circle were sampled for the first time. Scoured assemblages were, on average, 94.9% less abundant than those in undisturbed areas. The study at Adelaide Island also showed scour assemblages to be 75.9% less speciose than undisturbed assemblages. Ice disturbance has been considered for decades to be a structuring force on many polar communities, albeit due to anchor ice formation at high latitudes (Dayton et al. 1970), physical encasement of the intertidal zone (Waller et al. 2006) or icebergs grounding at depths of 0-500 m (McCook & Chapman 1993, Peck & Bullough 1993, Lenihan & Oliver 1995, Gutt et al. 1996, Conlan et al. 1998, Peck et al. 1999, Gerdes et al. 2003). Although I have simply made spatial comparisons and not measured post-disturbance community change *per se*, the results suggest iceberg impacts result in depauperate scour communities. Furthermore, by using only three sites as random factors in the univariate analysis, and still achieving significance, it can be can inferred that ice scour communities are likely to be lower in abundance and richness than undisturbed areas in other sites around Adelaide Island (and probably other similar polar locations). Iceberg impacts are likely to cause considerable changes in community structure and this, combined with the high frequency of impacts at nearshore polar locations (Brown et al. 2004, Smale et al. 2007a), suggests that ice scouring is a major structuring force acting on such communities.

Previous ice scour community studies, Arctic and Antarctic, have been in deeper water than the current study and have mostly concerned soft sediments (Conlan et al 1998, Gutt et al 1996, Gutt and Piepenburg 2003, Conlan & Kvitek 2005). The three sites in the current study varied in exposure and substratum type and, unsurprisingly, site had a strong influence on scoured and unscoured levels of abundance, richness and biomass. When scours were compared with undisturbed areas, species richness, biomass and the abundance of a number of taxa showed different patterns at the different sites. It is unclear whether this was due to the background source community at each site, or because of physical differences such as granulometry and disturbance

regime. However, it is clear that iceberg impacts were catastrophic at all sites, despite contrasting site characteristics. Nevertheless, (SCUBA) divers observed 'oases' of rich sessile communities on large boulders at all sites, which seemingly offered some protection in an otherwise highly disturbed habitat. The influence of substrate size and stability on assemblage richness, abundance and longevity has been well described (Barnes et al. 1996, Barnes & Clarke 1998), and whilst substratum type undoubtedly influences community development at Adelaide Island (Bowden et al. 2006) it may have little influence on the community change caused by catastrophic iceberg impacts.

Despite the high frequency of ice scour at all three sites (see Brown et al. 2004 and Smale, personal observations of old scours at Lagoon Bay, 2005), the unscoured communities sampled in this study were both rich and abundant. Over 100 taxa were found in a total sample area of 2.16 m^2 whilst abundance (site average) ranged from 755 ± 315 ind.0.09 m^{-2} at South Cove to 1694 ± 160 ind.0.09 m^{-2} at Hangar Cove. Barnes and Brockington (2003) also sampled a rich and abundant fauna at another site at Adelaide Island: they reported 75 taxa were in a 7.5 m^2 sample area and ca. 8000 ind.m^{-2} at 15m depth. Others studies have recorded similarly high richness and abundance values for shallow sublittoral communities in the Antarctic (Jazdzewski et al. 1986, Beckley & Branch 1992, Peck et al. 1999, Barnes et al. 2006). Although polar coastlines are amongst the most highly disturbed environments on Earth (Gutt & Starmans 2001), and their fauna typically slow growing and slow moving or sessile (Barnes 1995a, Peck et al. 1997, Brey et al. 1999) studies like the current one show that communities can still have both very rich and abundant benthos, even in relatively exposed conditions.

The most striking findings of the study concerned the composition of the scoured community. There are three mechanisms (locomotion, advection and larval recolonisation) by which fauna may return to a scoured zone, all of which work on different timescales (Peck et al. 1999). The maximum lag time between the ice scouring event and scour sampling was just 20 days, which is insufficient time for larvae to settle and mature (Pearse & Pearse 1991, Stanwell-Smith & Barnes 1997, Bowden 2005b), and no significant storms to induce advection currents were recorded

during lag times. The mean lag time between scour formation and scour sampling was 10 days, which is enough time for the abundant vagile members of the undisturbed community to move into the recently disturbed areas. Therefore, fauna found in scours had either (1) survived the iceberg impact or (2) arrived via lateral locomotion or (3) translocated from adjacent benthos via water movements caused by the grounding and/or retreat of the iceberg. It is likely that each of these forces contributed to the formation of the recently scoured community and that different taxonomic and trophic groups are influenced by different forces.

The small bivalve mollusc *Mysella charcoti* was often the most abundant species in scour communities. It is plausible that the heterogeneous morphology of iceberg keels resulted in small-scale patchiness and some chance of survivorship from impacts. Alternatively, small infauna may be 'cushioned' by surrounding sediment, again reducing the likelihood of total local community extinction from scouring. Other taxa prominent in the scoured community were either large (echinoderms) or motile (crustaceans and some molluscs). These faunal groups were plausibly the first to return by locomotion and/or advection currents and comprised largely of scavengers and deposit feeders. Conlan et al. (1998) reported an influx of deposit feeders and scavengers into new Arctic ice scours and ice-influenced shallows. Motile scavengers, such as lysianassid amphipods, are known to feed on detritus and damaged benthos in scours (Slattery & Oliver 1986, Peck et al. 1999, Conlan & Kvitek 2005) and they were found in both scoured and unscoured samples at all the study sites. Almost all scoured assemblages were low in biomass and contained small individuals, which could have survived the disturbance or been moved during the grounding event. The only exception being assemblages including the echinoid *S. neumayeri,* which formed aggregations in and around new scours at Hangar Cove.

Interestingly, the relative abundance of secondary consumers was not significantly elevated in scours at any of the study sites, although a non-significant difference was recorded at Hangar Cove. This contrasts with both scours in the Arctic (Conlan et al. 1998) and with anthropogenic disturbances such as dredge tracks (Currie & Parry 1996, Kaiser et al. 2000) which select for certain feeding guilds. Peck et al (1999) found only motile macrofauna (scavengers) in new scours at Signy Island until a storm reintroduced other taxa 102 days after the impact. In another study, Gerdes et al

(2003) described assemblages in the Weddell Sea that were thought to have been recently scoured. Assemblages consisted primarily of motile echinoderms and amphipods and juvenile polychaetes (see also Richardson & Hedgepeth 1977, Lee et al. 2001).

The patterns described in the current study differ markedly from such studies as the scoured assemblages, although distinct from the adjacent unscoured community, were generally not skewed toward certain trophic or taxonomic groups but were instead less speciose and abundant versions of the unscoured assemblages. There are perhaps three main factors influencing these contrasting observations. Firstly, the current study scours were small compared with previous studies; for example, the scours sampled by Conlan et al. (1998) were an order of magnitude larger whilst deep-water scour marks may be up to 15 km long (Hotzel & Miller 1983). Disturbed sediments within smaller scours are intuitively closer to undisturbed adjacent benthos; therefore increasing the chances of rapid relocation of fauna from undisturbed communities (i.e. effect of disturbance size, see Kaiser et al. 2001, Cristoni et al. 2004). Secondly, the scours of unknown age sampled by Gerdes et al. (2003) may support an assemblage at a distinct stage of recolonisation with a distinct faunistic composition. Over time, the scour assemblages sampled in the current study may become more similar to those in other scours. Finally, the current study sites are frequently disturbed (Brown et al. 2004) and perhaps much more intensely disturbed than the Weddell Sea (Gerdes et al. 2003) and Canadian Arctic (Conlan & Kvitek 2005) study locations. It seems likely that the source communities in the shallows of Adelaide Island have characteristics that allow them to respond rapidly to disturbance events.

In summary, ice scouring is catastrophic to shallow water benthic communities at Adelaide Is., and this is probably fairly typical for coastal Antarctica (away from floating ice sheets). It is difficult to predict the precise effects of ice scouring as factors such as disturbance size, random survivorship and the ability of the unscoured community to respond all interact to increase complexity. Iceberg scouring did not favour a taxonomic or trophic group but did select for 'small' taxa, which either survived the impact or were translocated into the scour soon after formation. Air temperatures around the West Antarctic Peninsula have increased rapidly over the past 50 years (Vaughan et al. 2003) and there is recent evidence of coincident

warming in the adjacent ocean (Meredith & King 2005). There has already been considerable and accelerated glacier retreat along much of the Antarctic Peninsula (Cook et al. 2005). Further warming is likely to increase the rate of retreat of maritime glaciers and perhaps promote the collapse of ice shelves, both of which would increase the number of icebergs in the coastal waters of the Antarctic Peninsula. This, in turn, may intensify the ice-mediated disturbance acting on benthic communities. The data presented in this chapter, along with reports of ice scouring from other locations, suggests that future changes in the frequency of ice scouring could result in considerable changes to benthic community structure in coastal polar habitats.

Chapter 5 – Community recovery following iceberg impacts

The data in this chapter are also published as: Smale D. A., Barnes, D. K. A, Fraser, K. P. P. and Peck, L. S. (in press) Community response to iceberg scouring at an intensely disturbed shallow water site at Adelaide Island, Antarctica. Marine Ecology-Progress Series.

Chapter 5 – Community recovery following iceberg impacts

INTRODUCTION

The immediate response of a community to a disturbance event, and its capacity to recover to a pre-disturbed state, are of major interest to ecologists. Disturbance events across spatial and intensity scales are known to play many roles in communities and ecosystems, not least in maintaining diversity (Connell 1978, Huston 1979). There are now many reports of significant changes in benthic community structure following both natural and anthropogenic disturbance events. For example, the effects of man's activities such as fishing practices (Currie & Parry 1996, Kaiser & Spencer 1996, Thrush & Dayton 2002) and oil spills (Jacobs 1980, Smith & Simpson 1998, Jewett et al. 1999) have been extensively covered, as have natural disturbances such as intense storms (Pearson 1981, Dollar & Tribble 1993) and feeding events (Oliver & Slattery 1985, Peterson et al. 2002). However, the timescales and processes involved in benthic recovery from one of the most widespread and intense forms of disturbance on the planet, ice scour, are poorly understood. Ice scour, the process of ice impacting the seabed, has been described as one of the five most significant disturbances acting at the ecosystem level (Gutt & Starmans 2001). In Antarctica alone, there are ~26,000 km of ice-shelf free shallow coastline, most of which could be impacted by one of the ~300,000 icebergs (Orheim 1987) that float around the Southern Ocean.

Iceberg impacts can be catastrophic (Lenihan & Oliver 1995, Conlan et al. 1998, Peck et al. 1999, Lee et al. 2001) and many shallow water polar communities are held at early successional stages by chronic ice scour (Dayton et al. 1974, McCook & Chapman 1993, Barnes 1995c, Pugh & Davenport 1997). Paradoxically, some major taxa inhabiting the highly disturbed nearshore environment around Antarctica are as rich, and in some cases richer, than those in tropical and temperate regions (Barnes & Brockington 2003). It has been suggested that ice disturbance has promoted biodiversity over ecological timescales by removing dominant competitors, increasing habitat heterogeneity and sustaining a diverse group of scavengers (Arntz et al. 1994, Barnes 2002, Gutt & Piepenburg 2003). On evolutionary timescales, ice disturbance may have promoted speciation by creating isolated refuges during glacial maxima (Held 2003, Allegrucci et al. 2006). However, it is currently unknown how long it

takes for a nearshore soft sediment assemblage to recover from ice scouring in the Southern Ocean. Understanding this process is of elevated importance at this time, particularly on the Antarctic Peninsula where air temperatures have risen by 3°C in the last 50 years (King & Harangozo 1998, Turner et al. 2005) and increased iceberg loading into coastal waters is a likely consequence.

Only one soft sediment Antarctic iceberg scour has been sampled over time to monitor community recovery. Following an initial >99.5% reduction in macrofauna, Peck et al. (1999) found no measurable recovery in some components of the disturbed community during the 250-day study period. Conversely, meiofauna had recovered to control levels within 30 days (Lee et al. 2001). In the Canadian Arctic, a comprehensive study by Conlan and Kvitek (2005) involving 19 iceberg scours at various stages of recolonisation suggested that >10 years is required for scoured communities to recover to background levels. No such data are available for shallow water Antarctic scours. A number of studies in the deep Weddell Sea, again using old scours at different stages of recovery, have highlighted the destruction caused by iceberg groundings and the resulting patchiness of the benthic system (Gutt et al. 1996, Gerdes et al. 2003, Gutt & Piepenburg 2003). In terms of post disturbance recovery, it seems that certain 'structural taxa' play a pivotal role during the successional stages required to return to a pre-perturbed state (Teixido et al. 2004). Growth rates are widely considered to be slow in the Antarctic (see Arntz et al. 1994, Barnes et al. 2007) and post-scour recovery may take an estimated 250-500 years for sponge dominated assemblages (Gutt & Starmans 2001).

In this study, patterns of post-disturbance recovery in three nearshore soft sediment iceberg scours were monitored for 30 months at Adelaide Island, West Antarctic Peninsula. This represents the first detailed observations of community response to iceberg scouring from within the Antarctic Circle.

METHODS

Study scours

Three distinct iceberg groundings were observed in Hangar Cove during the period March-July 2004. Each iceberg travelled from the north with the prevailing wind and remained grounded for ~48 hours. The position of each grounded iceberg was fixed with GPS and SCUBA divers marked the new scour once the iceberg had retreated (Fig. 5.1). The selected study scours were formed at ~14 m depth. Coloured pegs were randomly placed in the newly formed trough zones; these marks were subsequently used as sample points. Scour berms were not sampled because they were small and poorly formed. The scours were sampled at regular intervals for 30 months and the whole sampling period lasted from April 2004 to December 2006. Meteorological records collected at Rothera during the study period show that the average wind direction and speed were 006° and 12.5 knots (6.4 ms^{-2}) respectively.

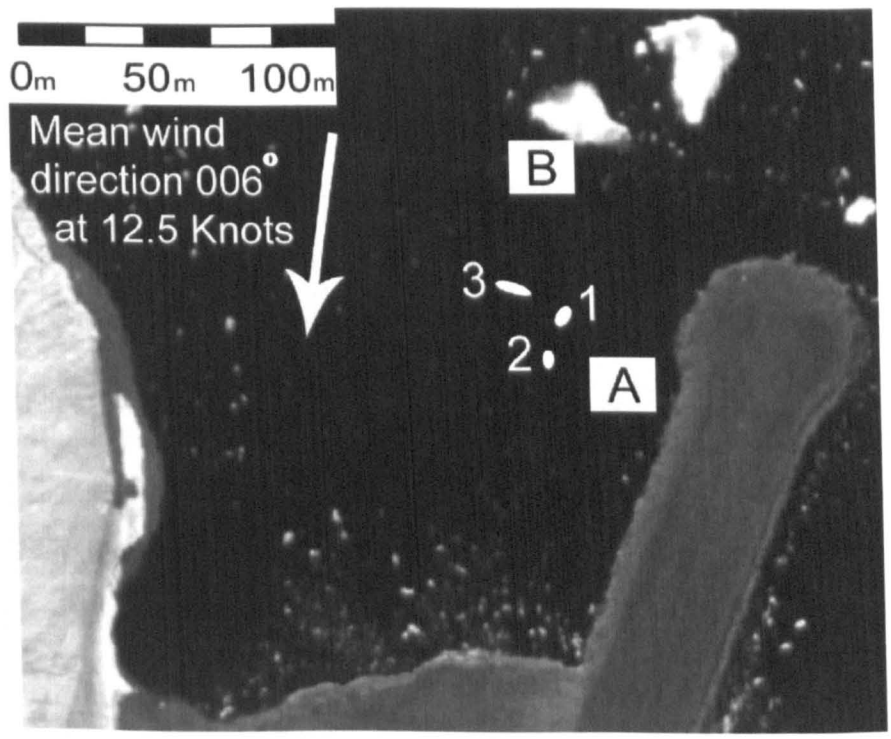


Figure 5.1 An aerial photograph of the Hangar Cove study site at Adelaide Island, Antarctica. Approximate positions, sizes and orientations of the study scours (labelled 1-3) are indicated. Box A indicates the 'sheltered' reference zone at 13 m and box B represents the 25 m depth sampling zone. Mean wind direction and speed are also shown.

Sampling protocol

The soft sediment layer at Hangar Cove varied in thickness from 0cm (exposed cobbles) to over 10 cm. Due to this heterogeneity, sediment sampling by traditional coring methods proved to be impractical. An aluminium scoop and mesh sampler was developed to sample 0.03 m^2 of the sediment to a depth of 2 cm. SCUBA divers collected 3 replicate samples from the impacted trough region of each scour. Three replicates were deemed sufficient to sample each scour adequately, despite the often-patchy nature of soft sediment biota, because scours at this site and depth were generally small. Samples were taken from each scour within 20 days of scour formation and subsequent recovery was monitored by sampling at 3, 6, 12, 18 and 30 months after impact. Two zones at the study site were identified in order to obtain unscoured reference samples. 'Sheltered ref' was at a similar depth (~13 m) to the scours but was protected from ice scouring by large boulders and an artificial airstrip, built in 1991. The '25 m ref' was deeper (25 m depth) and infrequently disturbed in comparison to shallower depths. Smale et al. (2007) quantified iceberg impact frequencies at Hangar Cove for 2 years and did not detect disturbance at this zone during the study period. No evidence of recent disturbance was found at either zone. An area of ~25 m^2 was marked out at each reference zone and the soft sediment assemblages were randomly sampled (n = 6) on three occasions during the study (Fig. 5.1).

Faunal analysis

Sediment samples were sieved through 0.5 mm mesh and preserved in 70 % ethanol. Samples were sorted to the lowest possible taxonomic level (typically species) immediately after collection. Organisms were blotted dry for 1 minute and then weighed to obtain wet mass measurements for estimating faunal biomass.

Statistical analysis

Mean values of total faunal abundance, species richness and total biomass were calculated from the three replicate samples from each of the three scours at each sampling occasion. Means of these parameters were also calculated from the two reference sites, to compare scoured and undisturbed communities over time. The mean abundances of higher taxonomic groups from both scours and reference zones were also plotted against time. All means are presented ± standard error (S.E). Error

bars represent S.E. in all figures, although in some cases only the positive bar is shown (for clarity). The differences in the abundances of major taxa between scour and reference samples at the both the initial sampling occasion and the final occasion were assessed with one-way ANOVA (using Minitab 14.0 software).

Multivariate analyses were applied using PRIMER v6, as described by Clarke and Warwick (2001) to determine underlying patterns to assemblage structure. Before generating Bray-Curtis co-efficient matrices, abundance data required square-root transformations to down weight the influence of two highly abundant species. The similarities between scoured communities and those at each of the reference zones at each sampling date were determined using one-way ANOSIM (Clarke, 1993). Replicate samples (n = 6) from the reference zones were averaged for each sampling event before comparisons were made. To illustrate increasing similarity between scour samples and reference samples during recovery, 1-ANOSIM R values were plotted against time (no negative R values were obtained), as done previously by Conlan and Kvitek (2005). Furthermore, a 2-way crossed ANOSIM test was applied to detect differences between scours groups over time (3 scour groups vs. 5 time groups) and reference groups over time (2 reference groups vs. 3 time groups).

Non-metric multidimensional scaling (MDS) was applied to assess the grouping structure of scour samples collected at each sampling occasion compared with reference samples, which were averaged for each sampling occasion. The multivariate dispersion of replicates within each sample set was determined using MVDISP. Taxa that contributed most to the observed differences were determined using the SIMPER procedure, which calculates the contribution of each taxon to the overall dissimilarity between two groups of samples (in this case scoured vs. reference).

RESULTS

Physical characteristics

Each iceberg grounding created a distinct scour mark in the substratum. Scours varied in length from 2.8 m to 5.8 m and in mean width from 1.1 ± 0.1 m to 1.8 ± 0.0 m (Table 5.1). Scours were elongated, with a mean width: length ratio of 2.7 ± 0.6. Initially the scours had a distinctive trough zone, which was slightly depressed and

characterised by recently exposed cobbles and patches of clay. Over time, the trough zones filled with fine sediment and biogenic matter and became less conspicuous. Each scour had a distinguishable raised berm but these features were generally small, poorly formed and became less pronounced throughout the study period.

Table 5.1 Length (L), width (W), depth (D) and date of the iceberg impact for each of the 3 study scours at Hangar Cove, Adelaide Is., WAP. Width is a mean of 3 random measurements ± S.E.

Scour	Length (m)	Width (m)	Depth (m)	Impact date
1	3.1	1.8 ± 0.0	14	23.03.2004
2	2.8	1.1 ± 0.1	13	15.06.2004
3	5.8	1.1 ± 0.3	15	01.07.2004

Univariate measures of community recovery

A total of ~33000 individuals representing 66 taxa were sampled. Most taxa were identified to species level, with the exceptions of one anthozoan, five ostracod specimens and all nematodes. Overall, small infaunal bivalve molluscs, polychaetes and nematodes, which formed 54%, 26% and 11% of all the individuals sampled, respectively, dominated the benthic community. Following each scouring event, faunal abundance and species richness were markedly lower in scours compared with reference zones. In comparison to a mean value for all the reference samples, macrofaunal abundance was ~96% lower in scours 1 and 2 and ~92% lower in scour 3. The number of species per sample following ice scouring were ~58%, ~64% and ~65% lower than in reference samples in scours 1, 2 and 3, respectively. However, variation in total sample biomass following scouring was not consistent between scours. When compared with the mean biomass of reference samples, scour 1 had a 280% higher biomass value on the first sampling occasion (t < 1 month). This was due to a number of the large regular echinoid *Sterechinus neumayeri*, which had formed aggregations in the recently formed scour after the iceberg had retreated. As high densities of large echinoids were not present in the undisturbed reference samples, post-scour biomass was considerably higher in this scour. Conversely, large echinoids were not sampled in scours 2 and 3, resulting in biomass values ~98% and 96% lower than in reference zones, respectively.

Over the 30-32 month sampling period, all three scours showed some recovery, in terms of abundance, towards the reference scours. Thirty-two months after the initial disturbance, faunal abundance in scour 1 had recovered to ~30% of reference abundances; scour abundance reached 190 ± 16 inds.0.03m^{-2} compared with a mean value of 637 ± 43 inds.0.03 m^{-2} from the reference zones. After 30 months, scour 2 had recovered to ~44% of the reference abundance whilst scour 3 was comparable to the reference zones at ~95% recovery (Fig. 5.2A). The number of individuals present in scour 3 showed a more linear increase (converging on undisturbed abundance levels) (Fig. 5.2A). Species richness recovered to levels comparable to the reference zones in considerably less time (Fig. 5.2B). The mean number of species present per sample (averaged across all sampling occasions) for the sheltered reference zone was 20.4 ± 0.7, whilst there were 18.1 ± 0.8 species present per sample at the 25 m depth reference zone. Richness in scours 2 and 3 were comparable after just 6 months (17.7 ± 1.7 and 17.3 ± 0.9 species per sample respectively) whilst scour 1 reached similar levels after 12 months of recovery (20.3 ± 1.5 species per sample). For the remainder of the study period both scours and reference sites stabilised at around 20 species per sample (Fig. 5.2B). Biomass values were highly variable between replicates, times and scours. Mass measurements were skewed by small numbers of the large echinoid *Sterechinus neumayeri* and the ophiuroid *Ophionotus victoriae*, which were present in some scours on some occasions. These taxa were rarely sampled at the reference zones and as a result the biomass values were much less variable between both replicates and times (Fig. 5.2C). Fig. 5.2C shows only the changes in biomass over time for scour 2, but demonstrates clearly the high variability and lack of a strong trend. Results for scours 1 and 3 were likewise highly variable and showed no clear trend.

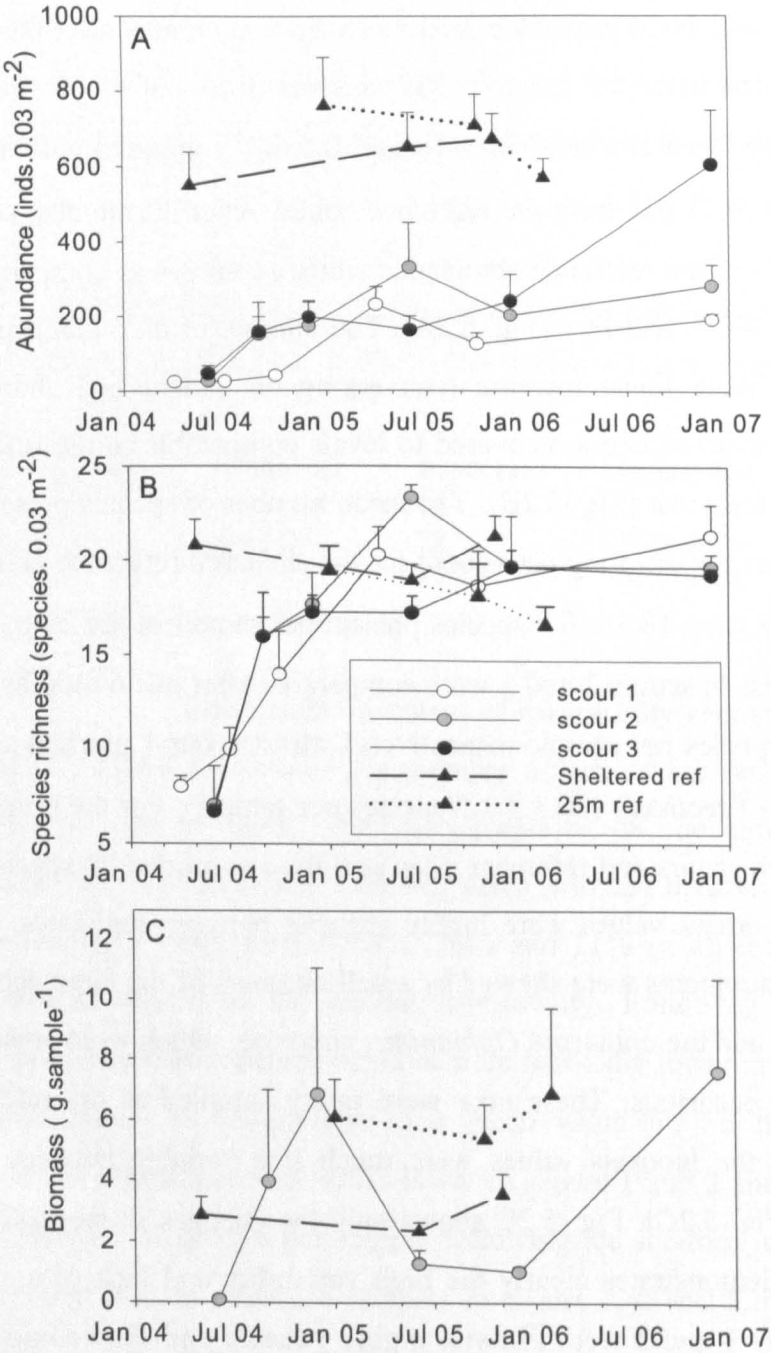


Figure 5.2 Total faunal abundance (A), species richness (B) and total biomass (C) of scour samples through recovery at Adelaide Island, Antarctica (means of 3 samples ± S.E). Scours were formed less than one month before the first sample point. Data from both sheltered and 25 m depth reference sites are also shown (means of 6 samples ± S.E).

Response of major taxonomic groups

Abundance data were separated into major taxonomic groups in order to identify taxon-specific trends in recovery following ice scour disturbance. The results of one-way ANOVA tests suggested that that each taxonomic group could be categorised in 4 ways: taxa that had significantly lower abundances in scours at the first sampling occasion time but were no longer different after 30-32 months (complete recovery); taxa that had recovered towards the reference zone abundance levels but were still significantly different after 30-32 months (incomplete recovery); taxa that demonstrated no clear trend; and taxa that had consistently higher abundances in scours compared with undisturbed zones (Fig. 5.3). Taxa showing characteristics of the first group (complete recovery) included the ostracods, polychaetes and uncommon worms (priapulans and nemerteans). At the first sampling occasion scour abundances were significantly lower than reference abundances (one-way ANOVA with 44 DF, ostracods: $F = 10.12$, $P = 0.003$; polychaetes: $F= 23.64$, $P = 0.000$; priapulans/ nemerteans: $F = 7.40$, $P = 0.009$). By the end of the study there were no significant differences in the abundance of these taxa between scour and reference samples (Fig. 5.3). The bivalve molluscs and nematodes demonstrated some recovery towards undisturbed abundances during the study, but were still significantly less abundant in scours after 30-32 months (bivalves: $F = 6.88$, $P = 0.012$; nematodes: $F = 8.13$, $P = 0.007$). Highly mobile crustaceans and gastropod molluscs showed no clear trend, as scour and reference abundances were not significantly different at the beginning or at the end of the study (Fig. 5.3). Echinoderm abundances were highly variable in scour samples, but echinoderms were generally more abundant in scours compared with reference zones.

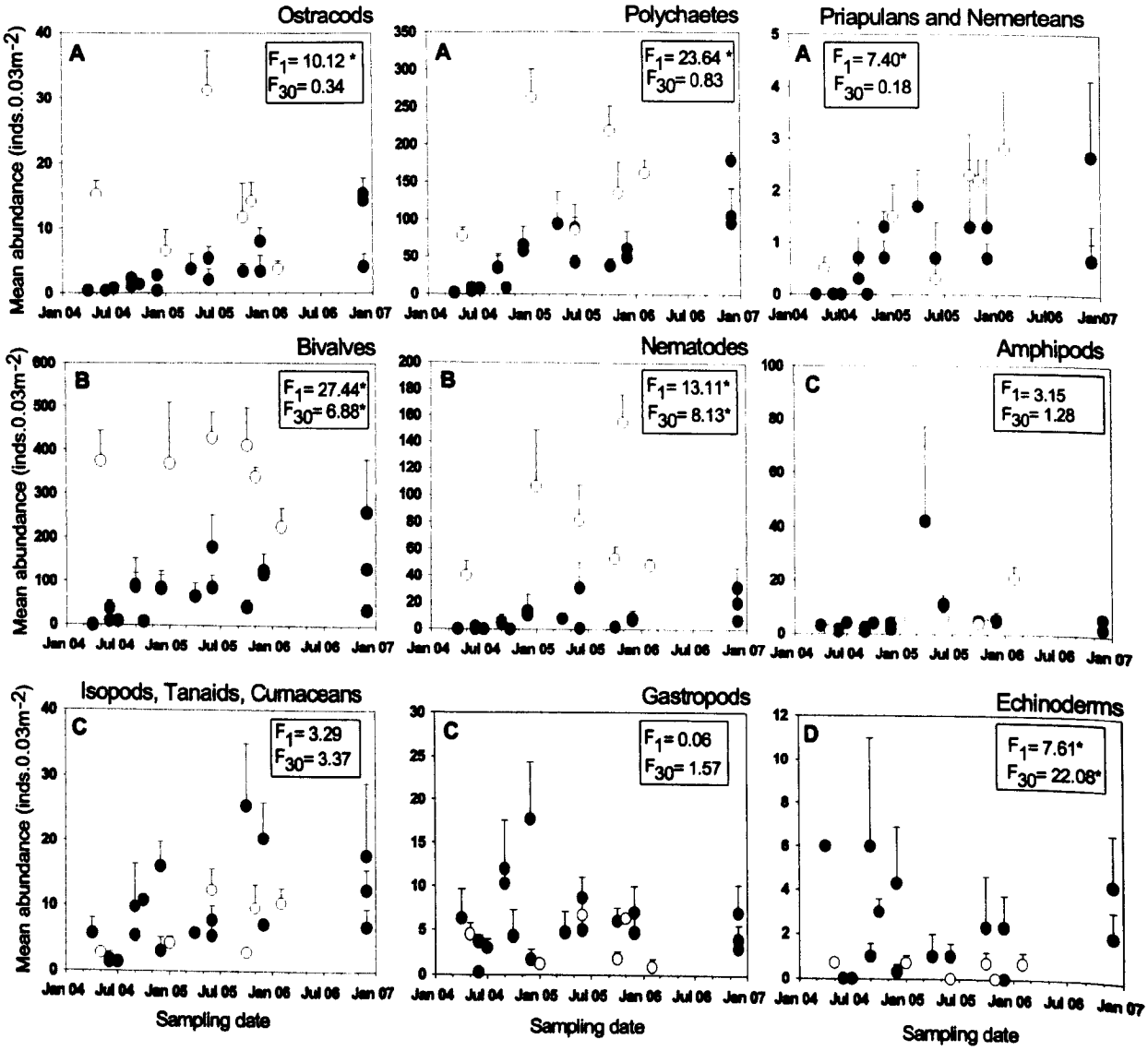


Figure 5.3 Post-disturbance changes in abundances of major taxa found in scours (black circles) compared with undisturbed reference abundances (white circles). Data are means ± S.E (scours n = 3, refs n = 6). Scours were formed less than one month before the first sample point. Differences in the abundance of taxa between all scour samples and all reference samples were tested with one-way ANOVA (total DF = 44) at 1 month after disturbance (F_1) and 30-32 months after disturbance (F_{30}). An asterisk (*) denotes significant F values ($P < 0.05$). Taxa showed either: complete recovery (A), incomplete recovery (B), no trend (C) or elevated abundances in scours (D).

Multivariate measures of community recovery

In all three scours, communities showed a general trend of increasing similarity towards reference communities over time. MDS ordinations of scour samples and samples from the sheltered reference zone demonstrated this pattern (Fig. 5.4). The MDS plots for each scour suggested that the samples collected on the first sampling occasion, within a month of scour formation, were well separated from all the other scour and reference samples. However, scour samples collected after 6 months of recovery were grouped considerably closer to the reference zone assemblages (Fig. 5.4). The MDS plot of all scours suggested some partitioning between both scours and reference zones. The significance of these groupings was examined with 2-way crossed ANOSIM tests (groups averaged across time), which suggested that scours were moderately distinct, but this spatial variation was comparable to that observed between the two reference zones (Table 5.2). Furthermore, a low but significant R value (0.28) showed that the reference assemblages were not entirely similar throughout the three sampling occasions (i.e. slight but significant background temporal variation was recorded).

A series of one-way ANOSIM tests between each recovery time group and each reference zone demonstrated a general trend in increasing similarity towards the reference community during the study period (Fig. 5.5). On the whole, recovering assemblages were more similar to reference zone B (at 25 m depth in the middle of the bay) than zone A (at a similar depth but more protected from ice scouring). Scour assemblages were highly dissimilar from those at the reference zones until 12 months of recovery time, when 1-ANOSIM values ranged from 0.07 to 0.32 compared with zone A, and from 0.31 to 0.71 compared with zone B (Fig. 5.5). Thus, with such high background spatial variability (between reference zones) these ANOSIM values indicated that assemblages in some of the scours were not particularly dissimilar from undisturbed assemblages after just 12 months of recovery. Furthermore, the variation within sample sets from each scour decreased over time (Table 5.3). Samples collected immediately after the disturbance events were highly variable, whilst after 30-32 months of recovery spatial variability within scours was comparable to that observed at the reference zones (Table 5.3).

Generally, species were either more abundant in the reference samples or uncommon in both scoured and undisturbed sediments. However, 5 species had notably greater mean abundances in scour samples compared to reference samples. The echinoid *Sterechinus neumayeri* was 5 times more abundant in scours than references zones (scours = 10 ± 3 inds.0.03m^{-2}, reference zones = 2.0 ± 0.3 inds.0.03m^{-2}). The other species more abundant in the scours were *Ophyrothrocha* sp. (scours = 9.0 ± 1.6 inds.0.03m^{-2}, refs. = 4.0 ± 1.2 inds.0.03m^{-2}), *Austrosignum glaciale* (scours = 0.8 ± 0.2 inds.0.03m^{-2}, refs. = 0.2 ± 0.1 inds.0.03m^{-2}), *Nototanais dimorphus* (scours = 4.5 ± 0.8 inds.0.03m^{-2}, refs. = 1.2 ± 0.3 inds.0.03m^{-2}) and *Eatoniella calignosa* (scours = 3.0 ± 0.7 inds.0.03m^{-2}, refs. = 0.7 ± 0.2 inds.0.03m^{-2}). The species that contributed most to the dissimilarity between scoured and reference samples were determined using the SIMPER procedure. Again, the dissimilarities at species level between scour and reference samples were greatly reduced at the final sampling occasion, compared with the first. The bivalve mollusc *Mysella charcoti* and the nematode group were consistently the highest contributors to the dissimilarity between the two sample groups (Table 5.4). These taxa were highly abundant in undisturbed sediments and did not recover in any of the scours to similar abundances during the study period.

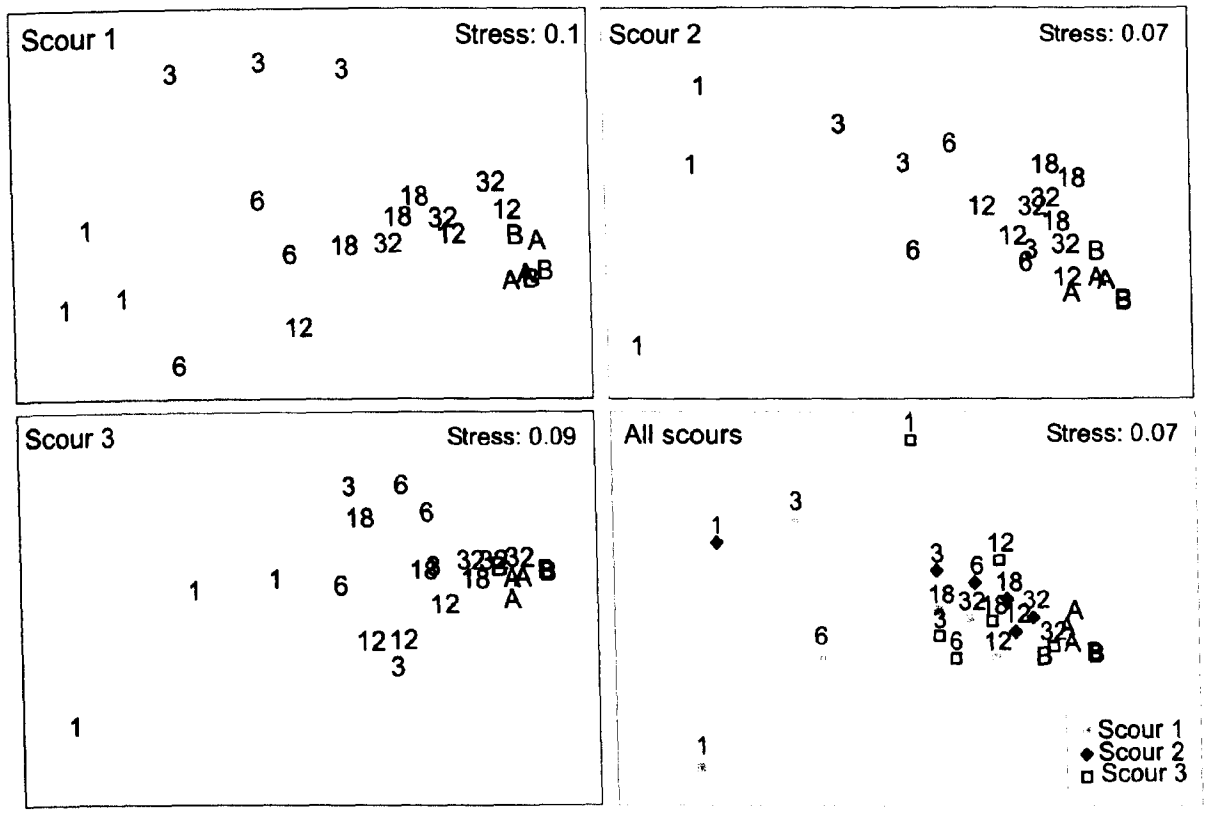


Figure 5.4 MDS plots of post-disturbance samples from each scour compared with reference samples (from sites A and B), collected from Adelaide Is., Antarctica. Scour samples were taken at <1, 3, 6, 12, 18 and 30-32 months following iceberg disturbance, as indicated by the sample labels. Final MDS plot shows averages of scour samples from all scours. Abundances were square root transformed before constructing a Bray-Curtis similarity matrix.

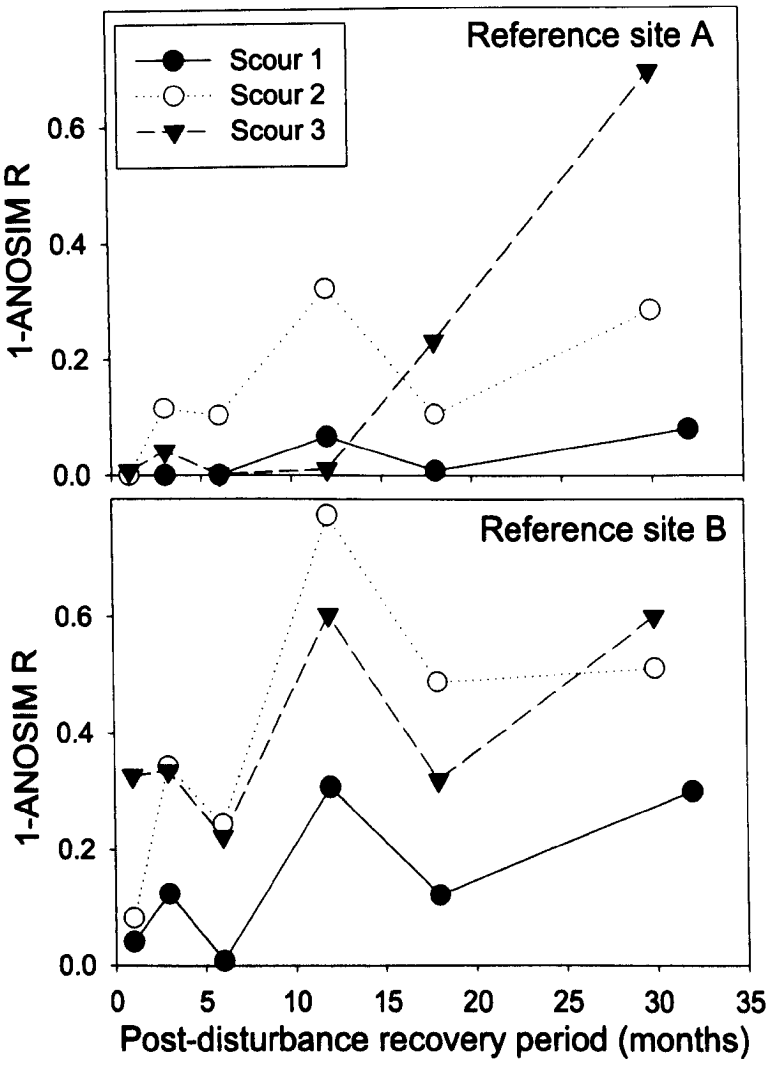


Figure 5.5 1-ANOSIM R values against post-disturbance recovery time for each scour sampled at Adelaide Is., Antarctica. Values are similarity tests between each sample time group and all samples from the reference zone A (top) and B (bottom). All results are significant at the 5% confidence level and were obtained from 999 permutations.

Table 5.2 Results of 2-Way Crossed ANOSIM R comparisons of scour, reference and time groups. An ANOSIM R value of 1 indicates sets of samples are entirely different, whilst a value of 0 suggests total similarity. R values calculated from 999 random permutations taken from large number. Scour time groups are 1, 3, 6, 12, 18 and 30-32 months following disturbance, reference time groups are 1-3 random sampling occasions conducted during the study.

Group	**R**	**P**
Scours across time	0.46	0.001
Pairwise:		
Scour 1 vs. Scour 2	0.59	0.001
Scour 1 vs. Scour 3	0.56	0.001
Scour 2 vs. Scour 3	0.32	0.013
Time across scours	0.51	0.001
Ref 1 vs. Ref 2	0.56	0.001
Time across refs	0.38	0.001

Table 5.3 Multivariate dispersion (MVDISP) values for each set of scour samples taken from each scour and at each sampling time (months following disturbance). A higher value indicates greater dispersion within the group of replicate samples. As the index is a relative measure, the values for the reference sites differ slightly when compared with each scour sample set.

	Scour		
Time	**1**	**2**	**3**
1	1.2	1.7	1.7
3	1.7	1.4	1.5
6	1.4	1.4	1.3
12	1.4	0.9	1.1
18	1.0	0.9	1.1
30-32	0.7	0.7	0.4
Ref A	0.3	0.5	0.4
Ref B	0.2	0.3	0.3

Table 5.4. Taxa responsible for differences between scoured and reference samples based on SIMPER analysis of square-root transformed data. Scour samples taken from each scour at the beginning of the study (<1 month after scour formation) and at the end of the study (30-32 months after scours formation) are compared with samples from the sheltered reference site. The five taxa that contribute most to the observed differences are shown. Total dissimilarity between groups is shown in parentheses.

Group	Taxa	%	Cum %
Scour 1 t1 vs Ref (94%)	*Mysella charcoti*	23	23
	Nematodes	11	34
	Aphelochaeta sp.	7	41
	Apistobranchus gudrunae	6	47
	Yoldia eightsi	5	52
Scour 1 t32 vs Ref (50%)	*Mysella charcoti*	21	21
	Nematodes	11	32
	Apistobranchus gudrunae	6	38
	Ophelina breviata	6	44
	Aphelochaeta sp.	6	50
Scour 2 t1 vs Ref (89%)	*Mysella charcoti*	23	23
	Nematodes	13	36
	Aphelochaeta sp.	7	43
	Apistobranchus gudrunae	7	50
	Yoldia eightsi	5	55
Scour 2 t30 vs Ref (37%)	*Mysella charcoti*	16	16
	Nematodes	12	28
	Aphelochaeta sp.	8	36
	Apistobranchus gudrunae	6	42
	Yoldia eightsi	4	46
Scour 3 t1 vs Ref (74%)	*Mysella charcoti*	21	21
	Nematodes	13	34
	Apistobranchus gudrunae	8	42
	Aphelochaeta sp.	7	49
	Scleroconcha sp.	5	54
Scour 3 t30 vs Ref (32%)	*Mysella charcoti*	10	10
	Nematodes	10	20
	Ophelina breviata	10	30
	Aphelochaeta sp.	10	40
	Apistobranchus gudrunae	7	47

DISCUSSION

Following each iceberg grounding, faunal abundance and species richness were markedly lower in the newly formed scours compared with undisturbed sediments. A ~95% reduction in faunal abundance was recorded at Hangar Cove, almost as great as the 99.5% reduction recorded by Peck et al. (1999) at a shallow water site at Signy Island. Furthermore, 1-ANOSIM R values for all scours at the first sampling occasion (<1 month after disturbance) were very low (<0.010), which shows that the recently scoured assemblage and undisturbed communities were almost entirely dissimilar. It seems that at Hangar Cove, iceberg scouring in soft sediments is catastrophic and results in significantly altered community structure. High benthic mortality caused by iceberg impacts in Antarctica has also been observed at Anvers Island (Richardson & Hedgepeth 1977) and King George Island (Bromberg et al. 2000), whilst collisions between ice and seabed are equally as destructive in Arctic waters (Conlan et al. 1998). Smale et al. (in press) gave a detailed account of the immediate effects of multiple iceberg groundings on the benthic communities at three contrasting sites at Adelaide Island; they reported an average reduction in macrofaunal abundance of 95% from 12 iceberg impacts (see Chapter 4 for full data set).

At Hangar Cove, many taxa returned to the scoured areas rapidly. Species richness and community structure in the scours was comparable to that in the reference zones after 12 months. Also, after the 30-month observation period no differences in the abundances of all crustacean groups (some of which had recovered within 20 days), gastropods and polychaetes between scours and reference zones were recorded. At Signy Island, South Orkneys, Peck et al. (1999) also reported the rapid return of some taxa into scours. Influxes of scavengers and detritivores into newly formed scours have been previously observed (Richardson & Hedgepeth 1977, Slattery & Oliver 1986) and a high abundance of motile scavengers inhabit Hangar Cove (Smale et al. 2007b). It seems that a considerable component of the benthic community at the study site are able to move rapidly into disturbed areas following iceberg retreat. Furthermore, the study site is exposed to the prevailing northerly wind at Rothera Point and as such is subjected to moderate wave disturbance and intense ice disturbance (Brown et al. 2004, Smale et al. 2007a). It is likely that small infauna, such as bivalves and gastropods, were advected into scours by water movements induced by grounding icebergs and wave action.

A number of species that were found in scours are known to be disturbance tolerant, and are well adapted to recolonise disturbed sediments. For example, the small burrowing polychaetes *Kefersteinia fauveli* and *Ophryotrocha* sp. were more abundant in scours than in undisturbed sediments. These polychaetes also have elevated abundances in sediments disturbed by anchor ice at McMurdo Sound (Lenihan & Oliver 1995, Conlan et al. 2004). Interestingly, the nematode group did not reach similar abundances in scours as in reference zones during the study, despite being well-known early colonisers of disturbed sediments in both high (Lee et al. 2001) and mid-latitude systems (Schratzberger & Warwick 1998, Wetzel et al. 2002). The reasons for this remain unclear, but nematode abundance was highly patchy in the reference zones and may reflect small-scale variation in organic content or particle size.

Conlan and Kvitek (2005) sampled 19 iceberg scours of different ages in the Canadian High Arctic. Scour assemblages reached 1-ANOSIM R values of 0.6 eight years after the disturbance event, whereas that value was recorded after just one year in the current study. The Arctic assemblages were richer than those at Hangar Cove (a total of 129 taxa compared with 66 in the current study) and the study sites were mostly in deeper water (and therefore almost certainly less disturbed by ice). The simple infaunal assemblages at the highly disturbed Hangar Cove study site are seemingly well adapted to responding rapidly to disturbance events. Also, the site is intensely disturbed and it is likely that even the reference zones, which were either in deeper water or partially protected, are impacted frequently enough to prevent the persistence of late successional stages.

Conversely, observations from the Weddell Sea shelf have suggested that scour communities remain distinct from adjacent undisturbed communities for decades (Gutt et al. 1996, Gutt & Starmans 2001). This is primarily due to rich, slow growing sponge assemblages dominating the undisturbed substratum, which is not the case at the shallow water Hangar Cove study site. Whilst many processes are thought to be slower in the Antarctic than elsewhere, it seems that some shallow water habitats are highly dynamic and benthic recovery may be surprisingly rapid. This could be of particular importance in the rapidly warming West Antarctic Peninsula region, where

decreasing sea ice duration (Vaughan et al. 2003), glacier acceleration (Pritchard & Vaughan 2007) and ice shelf retreat (Doake & Vaughan 1991, Scambos et al. 2000) are likely to increase the frequency of iceberg disturbance in shallow waters.

Finally, considerable small-scale variation in community structure at Hangar Cove was detected. The two reference zones, just 30 m apart, supported dissimilar assemblages whilst each scour assemblage was also distinct. Furthermore, variation between replicate samples was generally high. A number of factors may have induced variability in assemblage composition between scours including: the intensity of the iceberg grounding, community structure directly outside the scour, scour morphology and localised currents (Fig. 5.6). For example, a scour surrounded by a dense, rich assemblage will have a greater potential for quick colonisation than a scour surrounded by recently disturbed sediments. Furthermore, sediment, algae and detritus will be deposited at a faster rate in an elongated scour with raised berms than a wide shallow scour. An increased deposition rate and infilling of the scour depression would hasten community recovery and provide opportunities for deposit feeders and secondary consumers (Richardson & Hedgepeth 1977, Dernie et al. 2003). Other factors acting at small spatial scales that could influence the rate of recovery following iceberg impacts in Hangar Cove include: the input of algal matter from nearby substrata, the resuspension of nearby benthic organic matter by iceberg scouring (Peck et al. 2005), and the degree of heterogeneity of the trough substratum. On a regional scale, the input of organic matter from surface water production, seasonal fast ice duration and the number of recruits carried in by oceanic currents are likely to influence post-scour recovery.

Small-scale spatial variability is often the norm for shallow water soft sediment systems (Morrisey et al. 1992, Mannino & Montagna 1997), and Antarctic habitats are no exception (Stark 2000, Stark et al. 2003, Conlan et al. 2004). Whilst this variability complicates predictions of recovery rates and patterns, it is perhaps fundamental in promoting and maintaining benthic diversity, which is particularly high at the regional scale on the continental shelf of Antarctica (Arntz et al. 1997, Gray 2001, Clarke & Johnston 2003, Gutt & Piepenburg 2003). However, communities inhabiting intensely impacted sites such as Hangar Cove (Brown et al. 2004, Smale et al. 2007a) are likely to be held at fairly early successional stages

(McCook & Chapman 1993, Pugh & Davenport 1997). Also, the influence of small-scale patchiness in polar waters should not be overlooked when analysing data from lower-resolution, wider-ranging studies conducted at the regional scale.

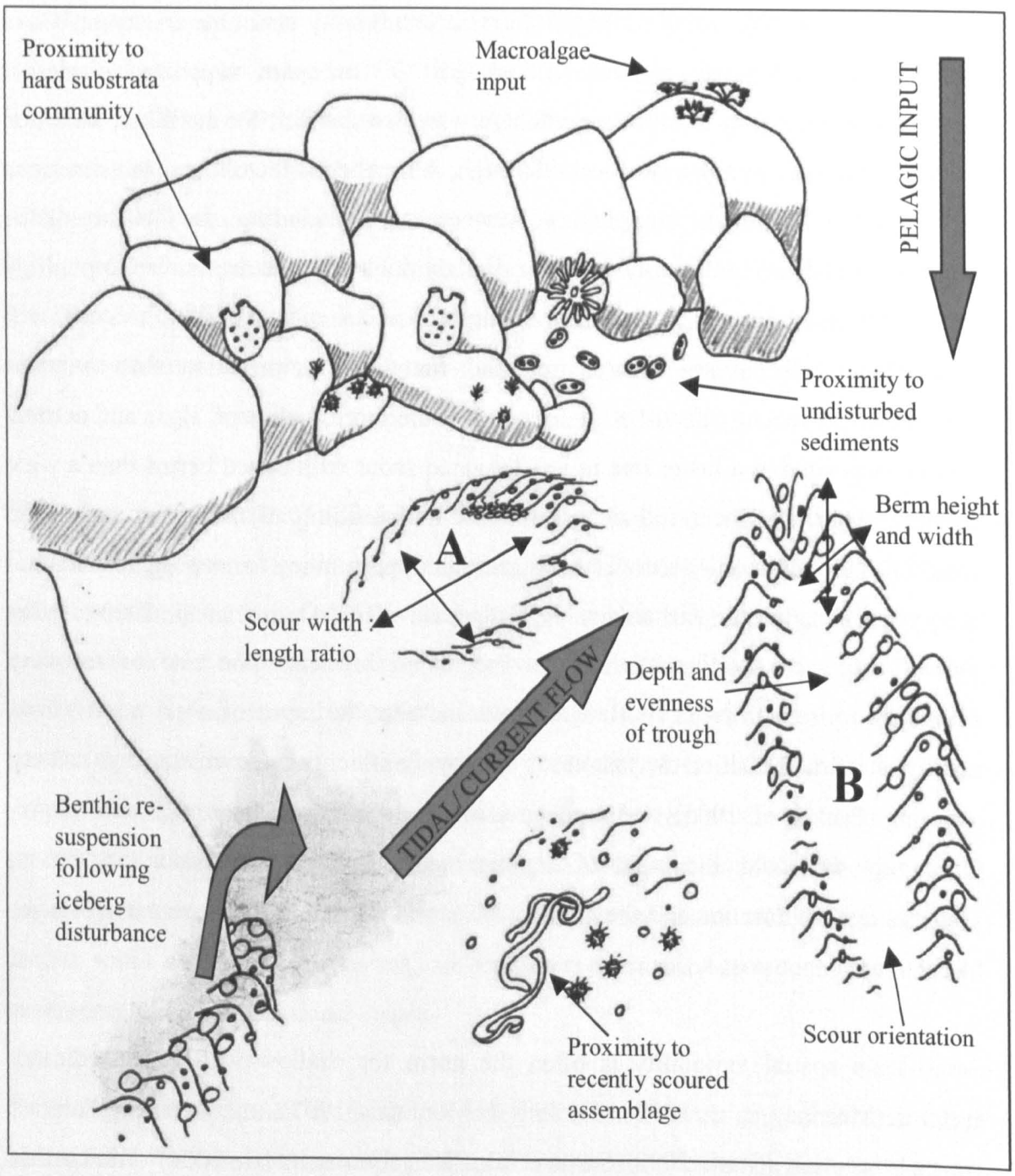


Figure 5.6 Schematic of major factors, acting at small spatial scales, potentially influencing post-scour community recovery at Hangar Cove, Adelaide Island, Antarctica. Potential factors influencing community recovery in two newly formed hypothetical scours (A and B) are shown. Jo Coldron is acknowledged for her contribution to figure 5.6.

Chapter 6 – A quantification of disturbance intensity

The data in this chapter is published as: Smale, D. A., Barnes, D. K. A. and Fraser, K. P. P. (2007) The influence of depth, site exposure and season on the intensity of iceberg scouring in nearshore Antarctic waters. Polar Biology 30: 769-779.

Dedication

This chapter is dedicated to Kirsty Brown, who died at Rothera on July 23rd 2003. Kirsty played a pivotal role in the development of the field technique during 2002 and 2003.

Chapter 6 – A quantification of disturbance intensity

INTRODUCTION

Icebergs are formed by the calving of ice from glaciers and ice sheets into marine waters and range in size from relatively small (~5 m height above the waterline) to massive tabular icebergs (~10,000 km^2). Ice scouring is caused by icebergs and sea ice contacting the seabed, resulting in physical alterations to the substratum (Woodworth-Lynas et al. 1991). The ecological effects of ice disturbance on benthic communities have been fairly well documented. Depth zonation of shallow subtidal communities caused by ice scouring has been reported at sites on the Antarctic Peninsula and Sub-Antarctic (Gambi et al. 1994, Barnes 1995c, Brouwer et al. 1995, Gambi et al. 2000, Nonato et al. 2000) and Arctic coastlines (Conlan et al. 1998, Conlan & Kvitek 2005). Exposed polar sediments may be completely reworked in 50 years (Reimnitz et al. 1977), resulting in high faunal mortality (Conlan et al. 1998, Peck et al. 1999, Lee et al. 2001), skewed population structures (Peck & Bullough 1993, Brown et al. 2004) and a dominance of mobile taxa and secondary consumers (Richardson & Hedgepeth 1977, Conlan et al. 1998, Conlan & Kvitek 2005). It has been suggested that every m^2 of the Antarctic shelf is disturbed once every 340 years (Gutt 2001) resulting in altered community structure and function (Gutt et al. 1996, Gutt 2000, Gerdes et al. 2003). Where ice disturbance is frequent and severe, communities can be held at early successional stages by chronic ice scouring (Dayton et al. 1974, McCook & Chapman 1993, Barnes 1995c, Pugh & Davenport 1997). However, intermediate levels of disturbance may promote biodiversity by preventing the monopolisation of space by dominant competitors (Barnes 2002, but see Bruno et al. 2003) and increasing habitat heterogeneity and niche separation (Brenner et al. 2001, Gutt & Piepenburg 2003).

The effects of depth and site on ice scouring frequency in the recent past have been inferred by seabed profiling of relict scour marks in both the Antarctic (Gutt & Starmans 2001) and the Arctic (Conlan & Kvitek 2005). Although the role of ice in structuring marine communities is well recognised (Gambi et al. 1994, Sahade et al. 1998, Gambi et al. 2000, Nonato et al. 2000, Barnes & Brockington 2003), there are

very few data concerning present-day scouring frequency. This is because such studies are both difficult and time consuming, and as of yet there have been no fully replicated studies on the influence of spatial and temporal factors on ice-mediated disturbance. Two previous techniques have been developed to measure ice scouring. Scrosati and Heaven (2006) developed a field technique involving small metallic cages, which were used to quantify the intensity of ice scouring at an ice-laden rocky shore in the Canadian subarctic. In another study, Brown et al. (2004) deployed concrete markers at a location on the Antarctic Peninsula to assess the disturbance regimes at two contrasting shallow water sites. The current study was an expansion of the work carried out by Brown et al. (2004), which further developed the field technique and used the same study sites. The aim of this study was to quantify the effects of depth, site exposure, and season on ice-mediated disturbance at a high-latitude polar location.

METHODS

Study sites

A series of 12 experimental grids comprising of 25 markers were deployed and monitored for two years at both South Cove and Hangar Cove. These sites were chosen for this study for their year-round accessibility and contrasting exposure to the prevailing wind direction at Rothera Point.

Impact markers

Each marker consisted of a cuboid concrete base (9 cm x 9 cm x 4 cm, ca. 750 g) with a non-toxic PVC-based modeling clay block (5 cm x 5 cm x 2 cm, ca. 85 g) secured onto the upper side. The clay block was secured to the concrete base with aluminum pins and silicon sealant. Markers were positioned on the seabed in order to detect iceberg impacts (see below). The marker design facilitated a hierarchal system of impact intensity, which could be assessed during SCUBA diving surveys. The malleable modeling clay component of the marker was used to detect low intensity iceberg impacts as low energy collisions leave visible deformations on the surface of the block. High-energy impacts destroyed the clay block and damaged the concrete base (Fig. 6.1). SCUBA divers assigned each marker an 'impact score' of 0-4 during surveys: (0) no damage to marker; (1) <50% clay section damaged; (2) >50% clay

section damaged; (3) concrete base damaged; (4) marker removed from experimental area or damaged beyond recognition (Fig. 6.1).

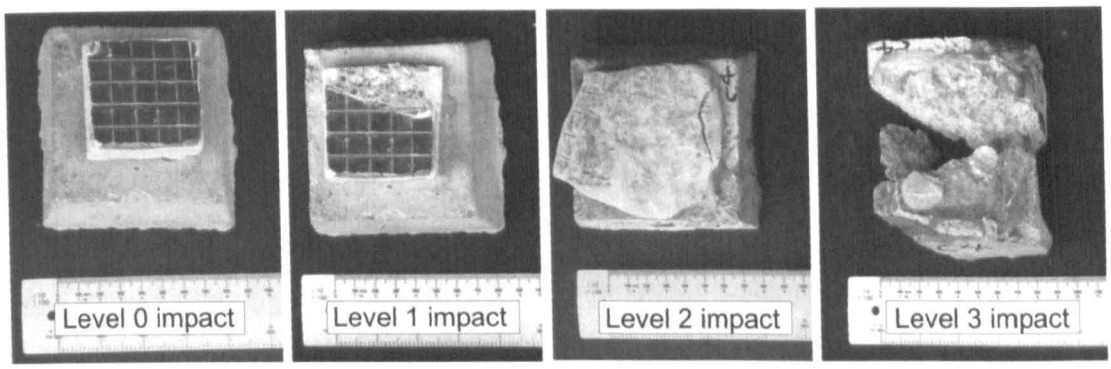


Figure 6.1 The experimental markers used to detect iceberg impacts and the scale used to measure disturbance intensity. Each marker had a concrete base and a standardised clay block attached to the upper surface. A 'Level 0' score indicated no recorded impact; a 'Level 1' impact resulted in <50% damage to the clay block; a 'Level 2' impact resulted in >50% damage to the clay block; a 'Level 3' impact caused damage to the concrete base. An intensity value of 4 was assigned to markers that were either destroyed beyond recognition or removed from the experimental area entirely.

Experimental design

Each experimental grid designed to measure iceberg disturbance consisted of 25 individual markers placed 1 m apart to cover an area of seabed 4 m by 4 m (i.e. 5 rows of 5 markers). Each marker was clearly labeled with a unique code to facilitate *in situ* identification and assessment. Three replicate grids were laid at water depths of 25 m, 10 m, 5 m and 0 m at both sites. These grids were laid along a depth gradient and therefore formed three replicate transects at each site (Fig. 6.2). The 0 m depth grids were laid on the rocky shore at Extreme Low Water Spring tide level (ELWS) whilst SCUBA divers deployed the subtidal grids. The grids were surveyed at 3 monthly intervals and any damaged markers were recorded and replaced. The grids deployed at ELWS (0 m depth) were surveyed, but not rebuilt, more frequently during summer, as the frequency of impacts was consistently high at this time. Disturbance data was gathered for the period January 2004 to February 2006.

Figure 6.2 Aerial photograph showing positions of disturbance grids at South Cove (A) and Hangar Cove (B). Numerals show transect numbers and symbols indicate depth increments.

Statistical analysis

Two measures were analysed, disturbance frequency (F_d) and disturbance intensity (I_d). F_d is simply the total number of impacts recorded per grid. I_d is the mean impact score per grid; therefore each grid generated a value ranging from 0-4 (and hence relating to the scale defined above) at each sample point. The scores for replicate sets of grids were pooled and tested for normality (Kolmogorov-Smirnov normality test). Although these data were effectively a proportion, (i.e. number of hits per grid out of a maximum of 25) examination of the residuals showed minimal heterogeneity of variance and therefore untransformed data were analysed. Each grid (of 25 markers) was treated as one statistical unit, thereby providing 24 units generating data over 8

time phases, all within a nested experimental design. Mean impact frequencies for depth were obtained by averaging depth replicates across all time phases. Means for sites and years were calculated by averaging across transects. All means are presented ± Standard Error (SE). The influence of depth, site, season and year on variance were analysed using a nested ANOVA design in Minitab 14.0.

RESULTS

Depth, site season and year were all significant factors affecting the intensity of iceberg scouring, I_d at Adelaide Island, Antarctica. Depth, season and year were accepted at the > 99.9% confidence level, whilst site was significant at the > 95% level (Table 6.1). The same factors also significantly influenced disturbance frequency, F_d (all *P* values > 0.05). Therefore, I_d is principally referred to as it relates to both the number and the intensity of iceberg impacts.

Depth

Disturbance frequency, F_d, decreased with depth at both study sites (Fig. 6.3). At both South Cove and Hangar Cove the most frequently impacted grids were those laid at the ELWS level (0 m depth grids). During the fast ice-free summer months, when brash and small icebergs were most mobile, 100% of the markers laid at the ELWS level were damaged on several occasions. For example, in January 2005, all 75 markers laid at ELWS (0 m depth) at South Cove were impacted by ice within 24 hours of placement. In contrast, impacts were recorded at the 25 m depth grids in just 2 of the 8 SCUBA diving surveys at each site. The mean number of impacts per grid at the 0m level (per 3 month survey) was 17.5 ± 0.1 at South Cove and 9.4 ± 0.0 at Hangar Cove, whilst the 25 m depth grids incurred an average of 1.5 ± 0.3 and 1.8 ± 1.7 hits per grid, at South Cove and Hangar Cove respectively. This indicates that floating ice impacted the rocky shore at Adelaide Island ~12 times more frequently than the seabed at 25 m depth at South Cove and ~5 times more frequently than 25 m depth at Hangar Cove (but see discussion re. ice foot disturbance). Depth also had a significant effect on disturbance intensity, I_d (Table 6.1). However, due to a number of high intensity impacts at deep grids at Hangar Cove, the 0 m depth I_d value was just 3.3 times greater than the 25 m value (Fig. 6.3).

Table 6.1 Results of nested ANOVA with disturbance intensity (I_d) the response to each factor and interaction. Table modified to allow for hierarchical structure of data due to transects nested within sites and repeated measures of year, season and depth within transects.

Source	DF	SS	MS	F	P
Site	1	1598.52	1598.52	10.85	0.030
Year	1	9102.52	9102.52	143.53	<0.001
Year*Site	1	204.19	204.19	3.22	0.15
Season	3	14890.94	4963.65	40.67	<0.001
Season*Site	3	5312.94	1770.98	14.51	<0.001
Season*Year	3	1125.02	375.01	4.70	0.022
Season*Site*Year	3	2659.69	886.56	17.80	<0.001
Depth	3	15349.35	5116.45	23.90	<0.001
Depth*Site	3	3221.85	1073.95	5.02	0.018
Depth*Year	3	2025.35	675.12	3.28	0.059
Depth*Season	9	3159.52	351.06	4.91	<0.001
Depth*Site*Year	3	2018.02	672.67	3.27	0.059
Depth*Site*Season	9	2874.35	319.37	4.47	<0.001
Depth*Year*Season	9	3888.44	432.05	5.88	<0.001
Depth*Site*Year*Season	9	5647.44	627.49	8.54	<0.001

Low, medium and high-level impacts were recorded at every depth at both sites. The distribution of low intensity impacts (level 1) and high intensity impacts (level 3) was examined at each depth increment by calculating the contribution of these impact types to the total number of hits recorded. The proportion of low energy impacts showed no relationship with depth, whilst the percentage of high intensity impacts showed a significant correlation with water depth (Fig. 6.4). Regression analysis showed that the proportion of high intensity impacts was significantly greater at 25 m depth than at the ELWS (0 m depth) grids ($F = 6.53$, $P = 0.018$, $R^2 = 22.9$).

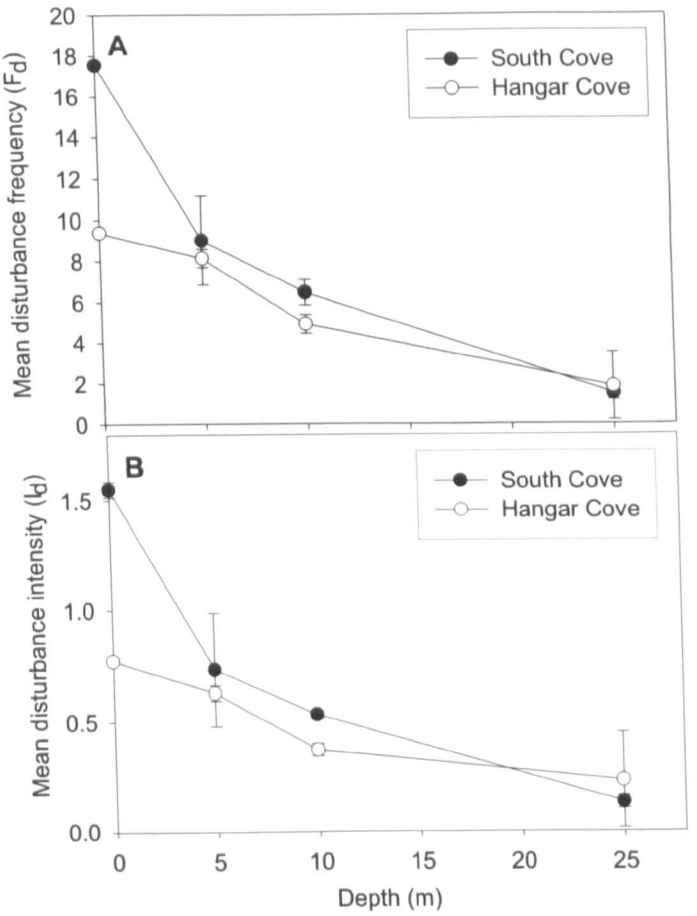


Figure 6.3 Mean disturbance frequency, F_d, (± SE) per grid (A) and mean disturbance intensity, I_d, (± SE) per grid (B) plotted against water depth at South Cove and Hangar Cove. Data are means for each 3 month survey period, averaged across the 3 transects at each site.

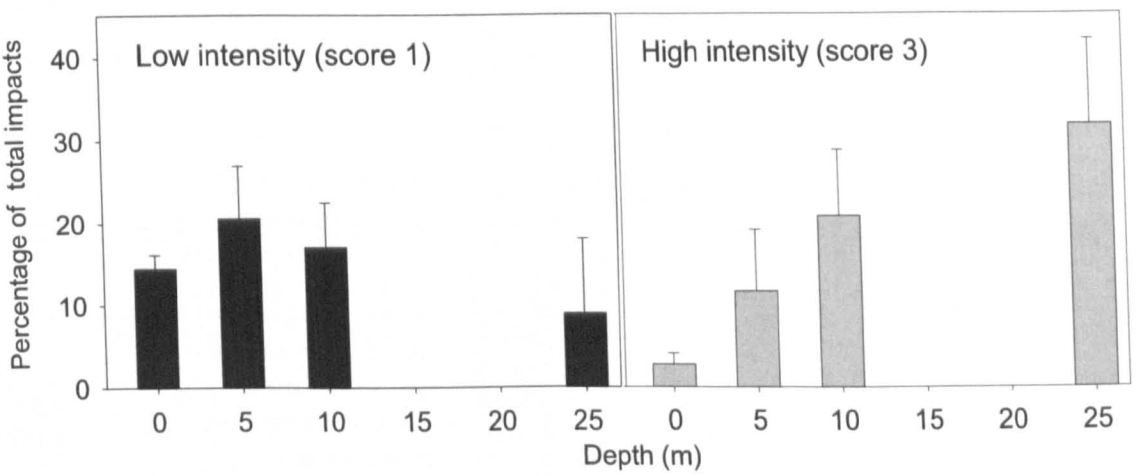


Figure 6.4 Percentage of total impacts that were low intensity (black bars) and high intensity (grey bars) at each water depth increment. Data expressed as means (± SE) of grids at both sites (n = 6).

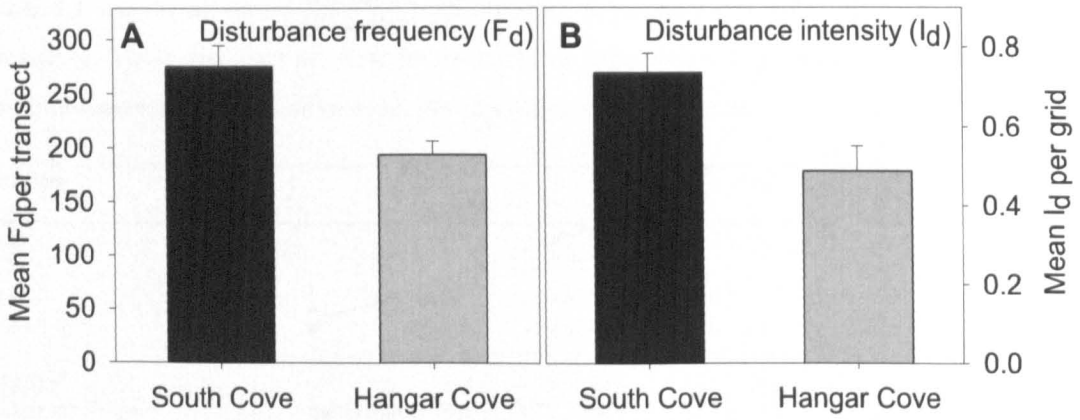


Figure 6. 5 Mean disturbance frequency, $F_{d,}$ (± SE) for each site (n = 3 transects) over entire study period (A). Mean disturbance intensity, I_d (± SE) for each grid within replicate transects at South Cove and Hangar Cove (B).

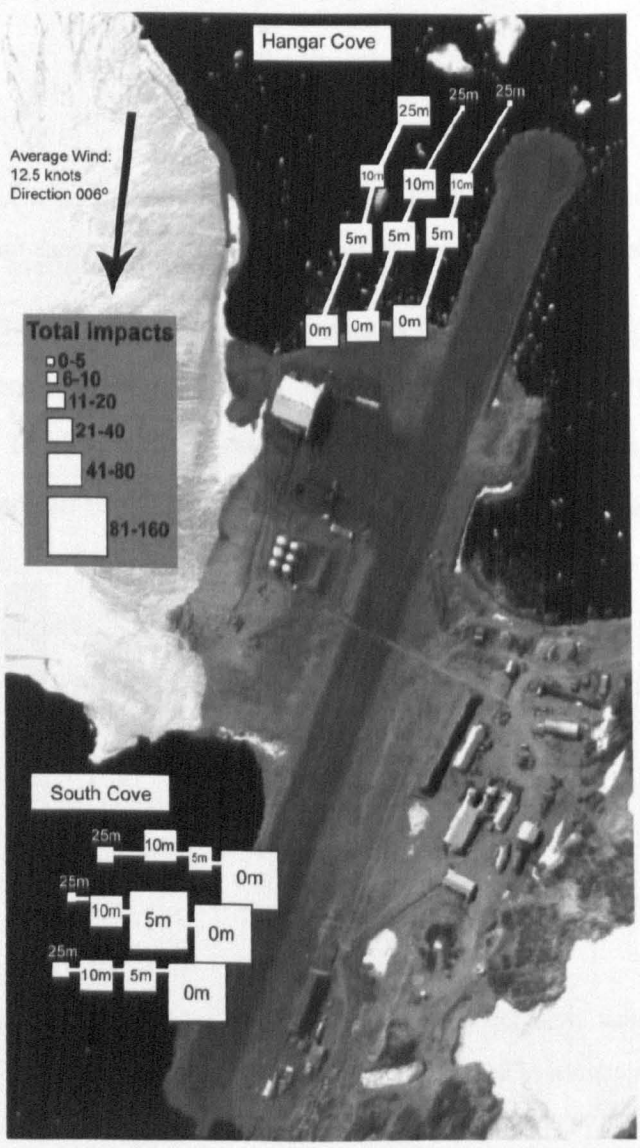


Figure 6.6 An aerial photograph indicating the positions of each disturbance grid at each study site. Accurate fixes of the grids were made using GPS. The area of the white square represents the total number of impacts (sum of frequency scores, F_d) recorded for each grid over the two-year study.

Site

The level of disturbance intensity, I_d, recorded at South Cove was significantly greater than at Hangar Cove ($F = 10.85$, $P = 0.03$). Both F_d and I_d were ~1.5 times greater at South Cove than Hangar Cove (Fig. 6.5). In terms of the number of markers hit during the study, 36% of the theoretical maximum were impacted at South Cove and 25% at Hangar Cove. The distribution of impacts was more homogenous at Hangar Cove, whilst at South Cove the gradient of depth and disturbance was more pronounced. These spatial patterns of total disturbance frequency (F_d) during the study period are illustrated in Figure 6.6. Generally, there was little variation in disturbance scores between replicate grids. However, the exceptions were the 5 m depth grids at South Cove and the 25 m depth grids at Hangar Cove, where the standard deviations of I_d were considerably greater than at other depths (Fig. 6.7).

Two factors likely to have influenced ice scouring during the study were wind and the timing and duration of winter fast ice formation, both of which were recorded. The average wind direction was 006° and average speed was 12.5 knots (or 6.4 ms^{-2}, BAS unpublished data). Therefore, Hangar Cove was more exposed to the prevalent wind and ice movements than South Cove. Winter fast ice formed in both years, but there was high variation between the study sites. In 2004, South Cove remained frozen for 81 days whilst fast ice was present at Hangar Cove for nearly two months more (135 days). The winter fast ice season was considerably longer in 2005, with 203 and 262 days of fast ice at South Cove and Hangar Cove respectively. In total, Hangar Cove had 1.4 times more sea ice days than South Cove (Table 6.2).

Table 6.2 Number of days of fast sea-ice at each study site and each year

	South Cove	**Hangar Cove**	**Total**
2004	81	135	216
2005	203	262	465
Total	284	397	

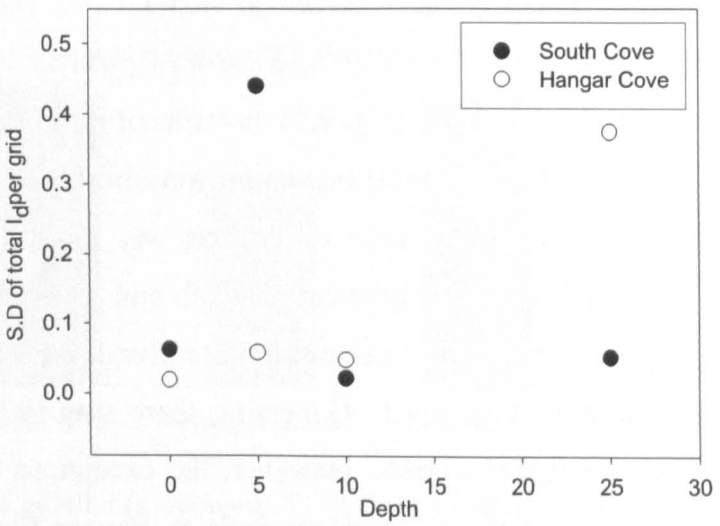


Figure 6.7 Standard deviations of total disturbance intensity scores I_d recorded the three replicate grids at each depth and site at South Cove and Hangar Cove.

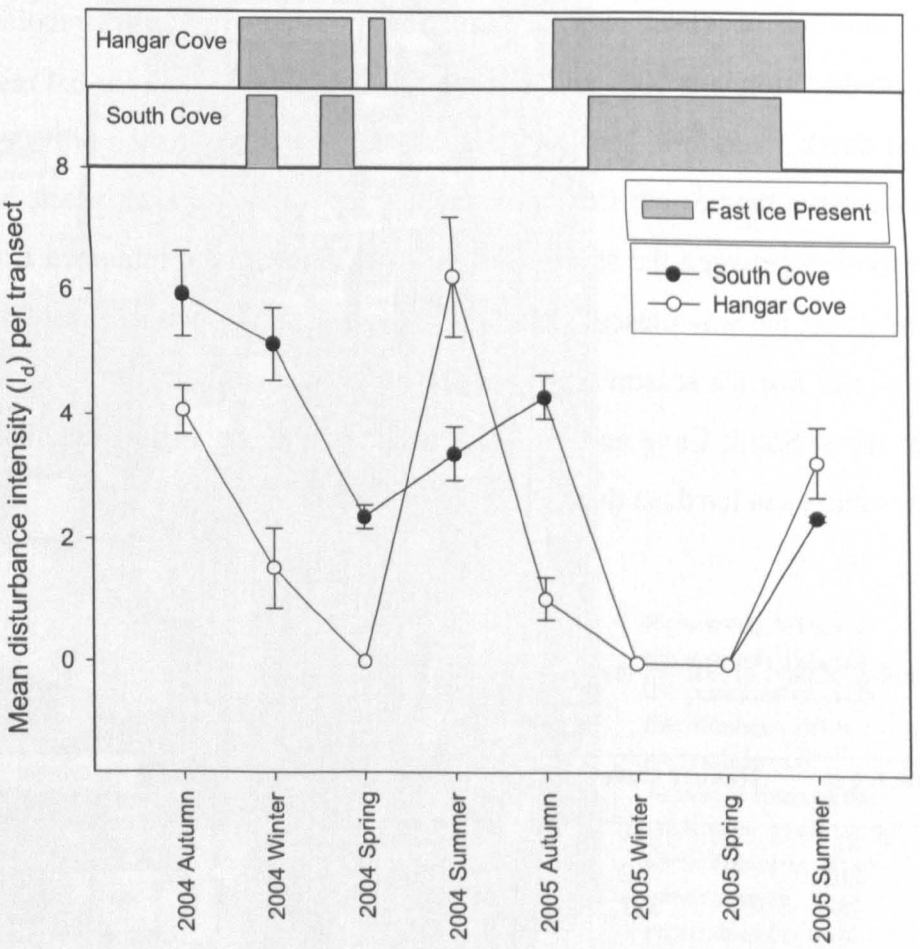


Figure 6.8 Mean disturbance intensity, I_d, (± SE) per transect plotted against each 3-month experimental phase at both study sites. Upper axis plots represent the presence of fast sea-ice at each site during the study period (grey areas).

Season and year

Disturbance from iceberg impacts showed a strong seasonal pattern, which was closely related to the formation of winter sea ice (Fig. 6.8). At both sites and in both years, the periods of maximum disturbance were the austral summer (Nov-Jan) and autumn (Feb-Apr). Both the F_d and I_d response variables significantly decreased during the winter (May-Jul) and spring (Aug-Oct) in both study years. No impacts were recorded at both sites for 6 months during winter 2005. However, the 0 m grids were encased in an ice foot during this period, which may represent a further disturbance pressure (see discussion). The greatest disturbance frequency was recorded at Hangar Cove in the 2004 summer survey, when 222 markers (74% of all markers) were hit. Season emerged as a highly significant factor influencing the disturbance score response ($F = 40.67$, $P < 0.001$) and interacted significantly with water depth, site and year (Table 6.1).

Disturbance intensity varied considerably between the two study years, with a 61% reduction in total I_d in 2005 compared with 2004 (Fig. 6.9). Year, like season, also emerged as highly significant and interacted with all other factors (Table 6.1). There were over twice as many days of sea ice (sum of both sites) in 2005 compared with 2004 (Table 6.2) whilst differences in wind speed and direction between the study years were negligible.

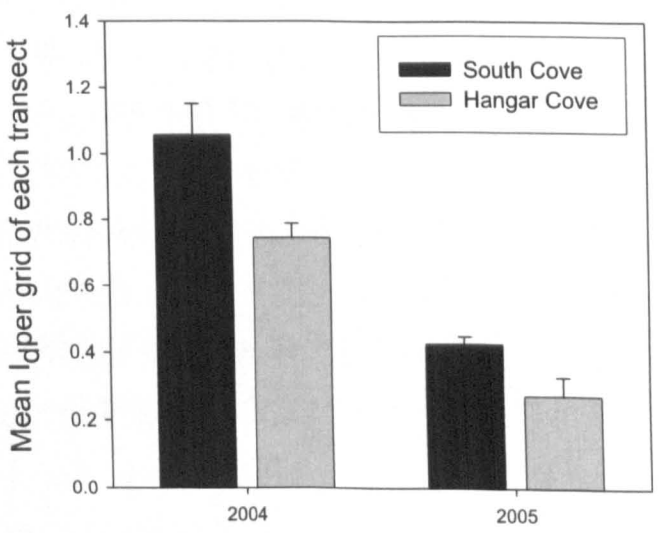


Figure 6.9 Mean disturbance intensity, I_d (± SE) per grid at both sites and for both years of the study at Adelaide Is., Antarctica. Means are averages of the three replicate transects at each site.

DISCUSSION

All the environmental factors (depth, site and season) had strong and significant effects on the frequency of ice scouring. Although the influence of some of these factors on ice scouring frequency may seem intuitive, this is the first time these relationships have been quantified at any shallow subtidal location. Over 1500 markers were impacted during the two-year study and this figure alone suggests that ice disturbance has a major structuring role on the ecology of nearshore polar waters.

Depth

A negative correlation between depth and the number of iceberg scours in polar continental shelf regions has been known for 20 years, since the use of sidescan sonar to detect relict scour marks (Lien et al. 1989, Dowdeswell et al. 1993). For the first time, the current frequency of ice scouring was measured and a strong relationship between depth and ice disturbance in nearshore polar waters ranging from 25 m to 0 m (ELWS) depth was recorded. In the Arctic, Hotzel and Miller (1983) observed a high frequency of icebergs with a low mass, height and length whilst large icebergs were less common. It seems likely that the size distribution of the iceberg population impacting the shores of the Antarctic Peninsula is also skewed towards a low mass. Thus the most likely explanations for a higher frequency of iceberg scouring at the shallow sites are two-fold. Firstly (and most intuitively), shallower sites were hit more frequently than deeper sites because small icebergs with small draughts were probably more frequent. Secondly, shallow sites were more exposed to scouring by winter fast ice and sea ice floes during break out periods. The markers laid at ELWS were frequently exposed to large rafts of sea-ice (maximum draft of ca. 1 m) during the springtime deterioration of annual fast ice. Hence, a strong environmental gradient of disturbance frequency with depth was recorded. Anchor ice is another form of ice disturbance and, like iceberg scouring, it is both depth-related and has a major structuring role on shallow water benthic communities (Dayton et al. 1969, Dayton et al. 1974). However, anchor ice was not observed at either site at any time during the current study.

The intensity of iceberg disturbance also varied with water depth, as high-level impacts (as a proportion of total hits) were more frequent at deep sites. A simple

calculation of the kinetic energy, E_k (Eqn. 1, where m is mass and v is velocity) of a typical iceberg impacting both the 25 m sites and the 0 m grids may explain this result.

$$E_k = (1/2)mv^2 \qquad \text{Eqn. 1}$$

The mass of an iceberg with a draft of 25 m (the minimum size needed to impact the 25 m deep markers) is estimated at 2.35×10^7 kg (Hotzel & Miller 1983), whilst an iceberg with a draught of 1m, a growler (Table 1), has a maximum mass of 1.20×10^5 kg (Haykin et al. 1994). To estimate the velocity of icebergs travelling into the study sites, the movement of 6 icebergs was monitored using time-lapse photography during a typical meteorological event with average winds of 22 knots. A mean velocity of 0.16 km/hr ± 0.02 was observed. Inputting the data into equation 1 gives an estimated kinetic energy of 22.75 kJ for the larger iceberg and 0.12 kJ for the smaller growler, an almost 200 fold reduction in energy. Although these figures are crude estimates and are prone to some error, they support the study observation that disturbance events at deeper sites are generally more energetic and intense than events at shallow sites.

It is important to note that the 'disturbance' values for the ELWS (0 m depth) grids were not an attempt to estimate total disturbance, as the methodology did not measure the physical effects of wave action and encasement of the ice-foot during winter. The ecological effects of wave exposure on intertidal and subtidal communities have been extensively studied (Underwood & Jernakoff 1984, Denny 1988, Dexter 1992). In the current study, exposure to wave action was not directly quantified, although the markers laid on the rocky shore would have detected wave-induced ice movements. Even though the study sites were both fairly sheltered from local swell and had a short fetch, wave action was another disturbance pressure acting on the intertidal rocky shore, which was unmeasured. The ice foot is a 'narrow fringe of ice attached to the coast' (WMO 1970) and is formed during winter as seawater meets the cold rocky shore and freezes. This layer of ice extends seaward and covers the intertidal and shallow subtidal, and remains for longer durations than seasonal fast ice. The encasement of the biota by the ice foot has a physical effect as it restricts the exchange of gases and water, equalises the temperature of the zone with ambient air

temperature and limits colonisation by new settlers to just a few months of the year (Barnes 1995b, 1999, Waller et al. 2006). However, the markers used to detect disturbance in this study were unaffected by the ice foot and most markers showed no signs of damage after up to 9 months of encasement. This contrasts with a study by Scrosati and Heaven (2006), which reported a widespread physical disturbance caused by winter sea-ice at an intertidal site in the Canadian subarctic. It seems probable that the crushing force of the ice foot at the study sites was disruptive, but not detected by the less-sensitive experimental markers deployed in this study. Effectively, only the abrasive action of brash, icebergs and fast ice on the rocky shore was measured. If one considers (and measured) all the disturbance pressures acting on the intertidal zone, (i.e. wave action and the downward force and physical barrier produced by the ice foot) the degree of disturbance acting on this rocky shore is likely to be much greater relative to the subtidal zones than reported here.

Site

The level of disturbance measured at South Cove was 1.5 times greater than at Hangar Cove over the 2-year study. Icebergs are transported by both wind action and water movements caused by ocean currents and tides (Rearic et al. 1990). The Hangar Cove site was exposed to the prevailing wind direction and hence wind-driven ice, whilst South Cove was more susceptible to ice transported by local current systems (personal observation). Ice scouring occurs primarily during periods without winter fast ice when icebergs are not 'locked-in' and are free to be moved around and impact the seabed (Barnes 1999). During the study period fast ice was recorded at Hangar Cove on 135 days, whilst South Cove was frozen for 81 days, a 1.6 fold difference. During winter 2004, fast ice formed at South Cove for a short period before breaking up after strong northerly winds, therefore exposing the site to incoming icebergs and pieces of sea ice. In comparison, Hangar Cove was frozen for much longer periods. It seems that the longevity of winter fast ice is a principal factor determining ice scouring frequency at these two study sites, and probably in shallow polar seas generally.

Both Brown et al (2004) and the current study observed some heterogeneity in the distribution of iceberg impacts at each depth increment. Small-scale changes in topography affect the local frequency of ice scouring in both deep water (Gutt & Starmans 2001), and (as is now evident) in shallow water. Although there was a

strong negative correlation between depth and disturbance, high variation in disturbance scores between grids laid at the same depth at the same site was recorded, particularly at the 5 m depth increment at South Cove (Fig. 6.6 and 6.7). For example, over the two-year study there was a three-fold difference in the number of hits recorded at two adjacent 5 m depth grids at South Cove. The grids were deployed about 20 m apart and it is likely that the variation was at least partly the result of small-scale differences in topography, substrate type or aspect. Interestingly, disturbance scores recorded at the 25 m depth grids at Hangar Cove were also highly variable. Whilst one grid received no impacts during the whole study another grid (again only 20 m away) was impacted 41 times. The substratum at Hangar Cove is much more uniform than at South Cove and offers little protection from ice scour. At this depth iceberg impacts seem to be rare and stochastic, resulting in a highly patchy distribution of disturbance events. In ecological terms, this spatial heterogeneity of disturbance events creates a mosaic of benthic assemblages at different stages of recovery. At large spatial scales this 'patchiness' of disturbance may promote biodiversity by increasing the number of available niches (Sousa 1979, Gutt & Piepenburg 2003, Conlan & Kvitek 2005).

Temporal factors

The formation and duration of winter fast ice had a significant influence on the frequency and intensity of ice scouring. Fast ice formation typically reduces disturbance by 'locking-in' icebergs, thus limiting periods of ice scour, and by preventing wave erosion (Barnes 1999). For the first time, the high degree of association between these two environmental factors was quantified. In 2005, there were twice as many days of sea ice and half the number of impacts compared with 2004. Even over a relatively short-term study, the intimate link between fast ice duration and ice scouring in shallow water habitats appears strong.

In the first study of its kind, Brown et al. (2004) estimated the frequency of ice scouring to be nearly three times greater at Hangar Cove compared with South Cove, which contrasts with the current study. Brown et al. (2004) deployed and monitored experimental marker for two years, from 2000 to 2002, over a limited depth range (ca. 10-15 m depth) and without replicated units. The reason for the higher frequency of ice scouring at Hangar Cove was inferred (but not stated) as being due to the exposure

of this study site to prevailing northerly winds (and therefore ice movements). Even when disturbance values for only the 10 m depth grids from the current study were analysed (a comparable depth with the previous study), the results from the two studies still conflicted. As the materials and methods used in both experiments were similar, and therefore generated justifiably comparable data, it seems that there is high inter-annual variation in the environmental conditions that govern the frequency of ice scouring at these high-latitude nearshore sites. Interestingly, the differences in inter-site scouring frequencies between Brown et al. (2004) and the current study cannot be explained simply by the number of fast ice days present during the study period. Fast ice was present for a total of 248 days at South Cove during 2001/2002 (BAS, unpublished data), whilst a similar number of 281 days was recorded during 2004/2005.

The duration of Antarctic fast ice varies between years (Clarke 1988, Jacobs & Comiso 1993) and decades (Murphy et al. 1995). Furthermore, there is some evidence that the extent and duration of Antarctic fast ice has decreased over the past century (Murphy et al. 1995, de la Mare 1997). Although estimates of sea ice cover from satellite observations available since the 1970s do not demonstrate a declining trend for total Antarctic sea ice (Jacka 1990, Cavalieri et al. 1997), satellite derived data have revealed a significant reduction in sea ice extent in the West Antarctic Peninsula region (Smith & Stammerjohn 2001). It is evident that the period of minimal seabed disturbance during the fast ice period is crucial for the development and growth of benthic communities (Barnes 1999). If there is a general decrease in the duration of fast ice at Adelaide Island, coupled with an increased scouring frequency, the implications for the already highly-disturbed shallow water benthos may be both wide-ranging and severe.

Sources of error and concluding remarks

The experimental markers and survey methods used in this study facilitated the quantification of ice-mediated disturbance and comparisons of relative scouring intensity between different depths, sites, seasons and years. However, the values were estimates of disturbance and there were several potential sources of error. Each marker was surveyed once every 3 months and damaged markers could have been impacted more than once during that time. Also, markers were placed 1 m apart and it

is possible that iceberg impacts occurred between markers and went undetected. Both of these eventualities would have resulted in an underestimation of ice scour frequency. Finally, each grid was treated as an independent unit for the purposes of replication and analysis. It is probable that scouring at one grid was not always independent of scouring at an adjacent grid, particularly when larger icebergs were causing the damage. Consequently, it is unclear how well correlated the experimental data are to the 'real' frequencies and intensities of ice disturbance at these sites. However, whilst this is a novel field technique, SCUBA divers have extensively visited the study locations for 10 years. During this time divers have observed many scour marks and qualitatively reported on depth-related and seasonal patterns of scouring frequency, which are supported by the experimental data presented here. It can be said with some confidence that the methods developed for this study; generate representative data, can be repeated across spatial and temporal scales, are adequately sensitive to detect long-term changes in disturbance patterns.

To summarise, the nearshore environment at Adelaide Island is disturbed by ice with great intensity and high frequency. Ice scouring has been described as one of the five most significant natural disturbances acting at the ecosystem level (Gutt & Starmans 2001) and it is undoubtedly a key structuring force acting at both small and large scales. The role of disturbance as a structuring force on natural communities has been well described (see Sousa 1984 for review). Although many disturbance pressures are difficult to quantify in space and time, the frequency of discrete disturbance events caused by ice scouring can be measured. The detailed quantification of ice-mediated disturbance presented here provided the opportunity to examine more fundamental ecological questions, such as the relationship between disturbance frequency and various parameters of community structure. The next chapter will examine the influences of each disturbance regime on the richness, abundance and structure of the benthic community.

Chapter 7 – Linking disturbance intensity with benthic community structure

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Chapter 7 – Linking disturbance intensity with benthic community structure

INTRODUCTION

Ice disturbance is a key structural force acting on shallow water benthic communities at high latitudes (e.g. Dayton et al. 1970, Peck et al. 1999, Brown et al. 2004, Conlan & Kvitek 2005, Smale et al. in press). However, until recently it has not been possible to study directly the influence of disturbance intensity on community structure, as quantifying ice disturbance is both logistically and experimentally challenging. Instead, proxies for disturbance such as depth (Barnes et al. 1996, Nonato et al. 2000), topographical protection from iceberg scouring (Sahade et al. 1998, Conlan & Kvitek 2005) and proximity to glaciers (Pugh & Davenport 1997) have been used to investigate the effect of ice disturbance on polar marine communities.

It has been suggested that where ice disturbance is frequent and severe benthic communities are held at early successional stages (McCook & Chapman 1993, Barnes 1995b, Pugh & Davenport 1997), dominated by mobile secondary consumers (Richardson & Hedgepeth 1977, Conlan et al. 1998, Conlan & Kvitek 2005) or fast-growing sessile pioneers (Barnes & Clarke 1998) and have skewed population structures (Peck & Bullough 1993, Brown et al. 2004). Furthermore, the intensity of ice disturbance, in the forms of encapsulation by the ice foot, ice scouring and anchor ice formation, is related (to varying degrees) to depth (Barnes 1995c, Lenihan & Oliver 1995, Smale et al. 2007a). As a result, many nearshore communities change continuously along a bathymetric gradient at high latitudes (Dayton et al. 1970, Gambi et al. 1994, Nonato et al. 2000, Barnes & Brockington 2003).

To date, only two attempts have been made to link empirical ice disturbance data with ecological parameters, one concerned anchor ice uplift and the second quantified iceberg scouring. Lenihan and Oliver (1995) used experimental stakes to assess the relative force of anchor ice uplift along a depth gradient. The shallow subtidal zone (4 m depth) was intensely disturbed by anchor ice and, as a result, was dominated by motile opportunistic infauna. Also, total densities of infauna and the number of

sedentary taxa were negatively related to the intensity of anchor ice disturbance (Lenihan & Oliver 1995).

Brown et al. (2004) used concrete markers to quantify the frequency of iceberg impacts in two adjacent coves at Adelaide island, Antarctica. Their study showed, for the first time, that a single point on the seabed at 10 m depth may be impacted by icebergs over three times in a two year period (Brown et al. 2004). One of their study sites was, on average, disturbed twice as often as the other, and encrusting bryozoan assemblages were less diverse, covered less space and were shorter-lived at the more frequently disturbed site (Brown et al. 2004). In chapter 6, the methods used by Brown et al. (2004) were developed and used to estimate the intensity of ice disturbance at 24 positions, across four depth increments and two sites, over a two-year period. The data showed that the frequency and intensity of ice disturbance varied significantly with depth, season and site. In this chapter, the benthos at each of disturbance grid locations used in chapter 6 was comprehensively sampled in order to make novel and detailed links between environmental parameters and benthic community structure. Two main hypotheses were tested, 1) measures of faunal presence (abundance, species richness, biomass and space coverage) all decrease with increasing intensity of ice disturbance, 2) ice-mediated disturbance is a key environmental variable influencing community structure in the Antarctic shallows.

METHODS

Study site

Sampling was conducted at Hangar Cove and South Cove at each of the 24 disturbance grids described in Chapter 6. For the current study, grids were additionally grouped into three classes based on total disturbance intensity (I_d) data; disturbance group 1 included the least disturbed grids (I_d = 0-100), group 2 related to moderately disturbed grids (I_d = 101-200), and disturbance group 3 consisted of the most intensely disturbed grids (I_d >201) (Table 7.1). Each disturbance grid covered an area of seabed of 16 m^2 and samples for the current study were collected randomly from within each disturbance grid.

Table 7.1 Summary of environmental data for each disturbance grid at South Cove and Hangar Cove, Adelaide Island, Antarctica. Disturbance data ('I_d') are total disturbance intensity values recorded during the 2-year survey. Disturbance intensity (I_d) was a measure of how frequently and severely markers within grids were damaged by iceberg impacts, as presented in chapter 6. The percentage cover of soft and hard substrata was estimated from ten 0.32 m^2 photoquadrats taken at each grid location.

Grid			Disturbance		Hard substratum
Site	Transect	Depth	I_d	Group	% cover
South Cove	1	0	311	3	100
	2	0	297	3	100
	3	0	322	3	100
	1	5	123	2	87
	2	5	244	3	92
	3	5	73	1	98
	1	10	109	2	96
	2	10	108	2	74
	3	10	101	2	90
	1	25	27	1	91
	2	25	17	1	61
	3	25	38	1	75
Hangar Cove	1	0	201	3	100
	2	0	206	3	100
	3	0	201	3	100
	1	5	128	2	73
	2	5	113	2	81
	3	5	136	2	76
	1	10	76	1	97
	2	10	83	1	80
	3	10	64	1	89
	1	25	0	1	2
	2	25	7	1	19
	3	25	133	2	18

Sampling design

Bowden (2005) showed that at these sites (and probably generally), sampling resolution had a significant effect on the type and size of fauna detected and analysed. The benthic communities at each disturbance grid were sampled at three levels of resolution. The methods described below were repeated at each of the 24 disturbance grids. Therefore, a total of 240 photoquadrats, 72 benthic samples and 240 rocks were analysed.

Megafauna. Twenty digital photoquadrats were taken at each grid. From this pool, ten photoquadrats were randomly selected for analysis. A Nikon D100 digital SLR camera fitted with Nikkor 12-24 mm DX lens was housed in a Nexus D100 casing

and used throughout. Lighting was achieved by a single Nikonos SB105 flash unit fitted with a diffuser. A carbon fibre framer was fitted to standardise the area sampled and to ensure the camera remained perpendicular to the seabed. Each image was cropped to give a sample area of 0.32 m^2 and all discernible fauna greater than 5 mm in size were identified to the lowest possible taxonomic level. All individuals of solitary taxa were counted, whilst modular taxa (sponges, bryozoans and ascidians) were quantified by the number of colonies/ units.

Macrofauna. At South Cove, which consists primarily of cobbles and patches of silt, three replicate 0.03 m^2 randomly placed quadrats were hand cleared by SCUBA divers. The silt layer at Hangar Cove was too thin to core effectively so a scoop and mesh sampler was used to sample a 0.03 m^2 area of sediment to a depth of 2 cm. Again, 3 samples were collected from each disturbance grid. All samples were sieved through a 0.5 mm mesh, coarsely sorted and preserved in 70% ethanol. Specimens were sorted to a minimum of family level, although most taxa were identified to species. All taxa were counted for abundance values and wet weights for all fauna were obtained for biomass analysis.

Encrusting fauna. Twenty cobbles (i.e. 64-256 mm in diameter, Wentworth 1922) were collected by SCUBA divers from each grid. From this pool of rocks 10 were selected at random, dried, labelled and later analysed. The surface area of each rock was estimated using graph paper. Bryozoans were identified to species level and abundance (number of colonies) and areal coverage were recorded for each rock. The abundances of other encrusting taxa (principally serpulids and spirorbids, but also sponges) were also recorded.

Environmental variables. The community parameters measured from the three scales of sampling described above were related to three environmental variables; depth; intensity of disturbance (and the resultant groupings, as presented in Chapter 6); and the percentage availability of different habitat types (bedrock and semi-stable substrata as opposed to soft sediments) at each grid. The percentage cover of each substratum type was estimated by projecting a grid onto the ten photoquadrats collected for the macrofauna survey. Although this was a rather crude estimation, it allowed the inclusion of a broad-scale measure of substratum type in the analysis.

Statistical analysis

Replicate samples from each disturbance grid were pooled to give megafaunal abundance and species richness per 3.2 m^2, macrofaunal abundance, species richness and biomass per 0.09 m^2, and cryptofauna abundance, species richness and percentage cover per 10 rocks. Initially, sites were pooled to test the validity of the disturbance groupings, but were then treated separately for analysis. The relationships between these univariate biological parameters and the environmental variables were assessed using regression analysis in Minitab 14.0 (significance accepted at $P < 0.05$ for all tests). Continuous disturbance data were used for regressions, whilst the disturbance groupings were used for multivariate tests.

Multivariate analyses of community structure were performed using the Primer v. 6 statistical package. Bray Curtis similarity matrices were produced based on the abundances of megafauna, macrofauna and encrusting fauna, which were pre-treated with fourth root transformations to down-weight the influence of highly abundant taxa. The relatedness of the communities at each grid was assessed using multidimensional scaling (MDS), whilst the strength of the groupings of depth, disturbance and site factors was tested using the two-way analysis of similarities (ANOSIM) procedure.

The BIOENV routine, which correlates environmental data with differences in community data (following normalisation of environmental data and the construction of a matrix based on Euclidian distance), was applied to determine which physical factor (depth, disturbance or hard substrata cover) best explained the observed patterns in community structure. Finally, a model matrix generated from similarities in disturbance groupings was correlated with the biological matrices using the RELATE routine. Finally, the species contributing most to the observed differences between disturbance groups were determined using the similarity percentages (SIMPER) analysis.

RESULTS

A total of 126 taxa were recorded (Appendix 1); 36, 94 and 16 different taxa were identified from the megafauna, macrofauna and encrusting fauna surveys, respectively (21 taxa were recorded at more than one sampling level). Fourteen phyla and 22

classes were represented by these taxa. Approximately 11,000 individuals were counted in megafauna samples, ~21,000 in macrofauna samples and ~40,000 encrusting individuals/ colonies were counted on rocks. Initially, the validity of the disturbance groupings on biological data was assessed by generating cumulative species dominance plots (*k*-dominance curves) for each disturbance group at each sampling level (Fig. 2). As could be predicted, *k*-dominance curves for disturbance group 3, which included samples from the most intensely disturbed grids, were consistently elevated; indicating that dominance was greater and diversity lower in these samples compared with those in disturbance groups 1 and 2 (Fig. 7.1). Conversely, plots for the least disturbed samples (group 1) were higher in diversity and less dominated by a small number of species. These patterns suggested that the disturbance groupings, applied to the biological samples on the basis of the disturbance intensity data (I_d), were ecologically relevant and therefore a suitable grouping structure for further analysis.

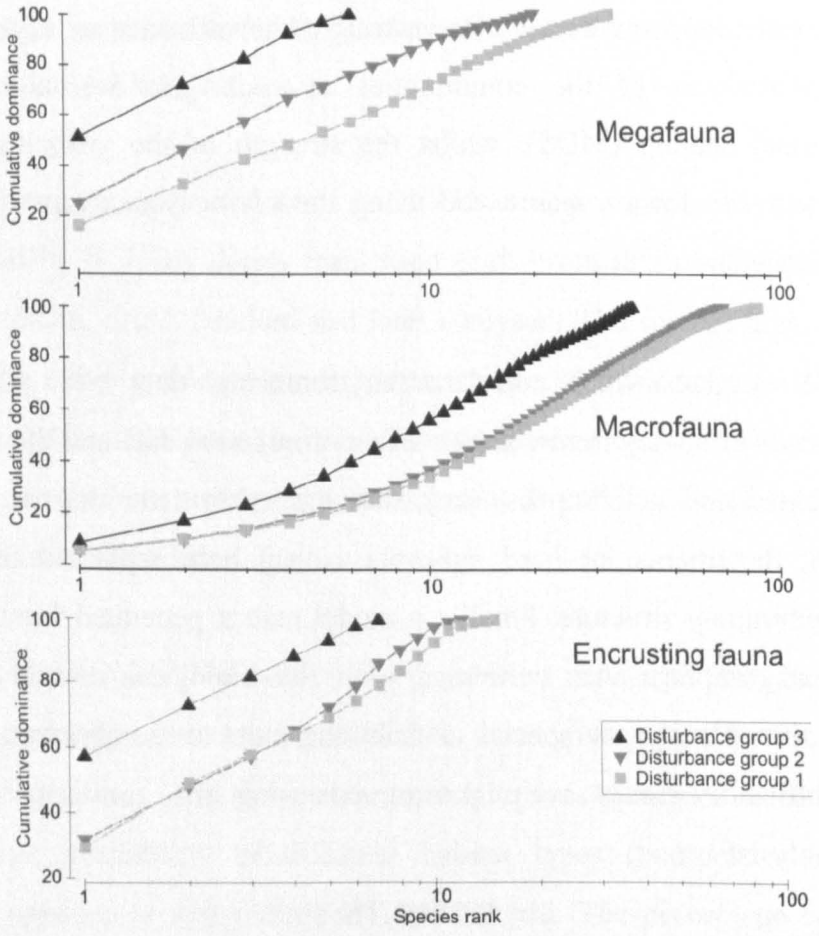

Figure 7.1 Cumulative species dominance curves (both sites pooled) at each sampling level for each disturbance group at Adelaide Island, Antarctica. Disturbance group 1 relates to grid locations that were least frequently disturbed, whilst grids in group 3 were most disturbed.

Regression analysis was used to explain the relationships between disturbance intensity and univariate patterns of community structure at the grid locations. Abundance, species richness, biomass and areal coverage were all significantly inversely related to the intensity of disturbance at South Cove (Fig. 7.2). At Hangar Cove, no significant relationship between disturbance and macrofaunal biomass and encrusting faunal species richness was recorded, whilst the other 6 biological parameters were negatively correlated with disturbance (Fig. 7.2). The strongest correlations were found at South Cove; species richness data at all sampling levels decreased significantly with increasing disturbance intensity (all R^2 values > 79.0, all P values < 0.001), whilst macrofaunal abundance ($R^2 = 68.4$, $P < 0.001$) and biomass ($R^2 = 83.5$, $P < 0.001$), and encrusting faunal areal coverage ($R^2 = 63.9$, $P = 0.002$) all decreased exponentially with increasing disturbance. At Hangar Cove, correlations between disturbance intensity and community parameters were generally weaker compared with South Cove. Even so, megafaunal abundance ($R^2 = 58.8$, $P = 0.004$), macrofaunal abundance ($R^2 = 62.4$, $P = 0.002$) and richness ($R^2 = 68.9$, $P < 0.001$), and encrusting faunal abundance ($R^2 = 55.3$, $P = 0.006$) all demonstrated strong inverse linearity with disturbance intensity (Fig. 7.2).

Multivariate analysis of species abundance data indicated that assemblages were significantly different between sites at the megafauna sampling level (two-way ANOSIM with site and depth, Global R for site = 0.852, $P = 0.001$), macrofauna sampling level (Global R for site = 1, $P = 0.001$) and the encrusting fauna sampling level (Global R for site = 0.315, $P = 0.006$). MDS ordinations of samples from each grid also suggested some grouping structure based on depth (Fig. 7.3), and Global ANOSIM R values for depth were >0.5 and highly significant at all sampling levels. For example, megafauna and macrofauna assemblages at 0 m depth were low in both the number of species and density of fauna compared with other depths and this is reflected in the distinct groupings of these samples. Intuitively, as depth and disturbance intensity are broadly correlated (Chapter 6) an overlaying bubble plot of disturbance intensity suggested that, to some degree, the samples on the MDS ordinations were also arranged along a disturbance gradient. This was particularly evident for encrusting fauna (Fig. 7.3).

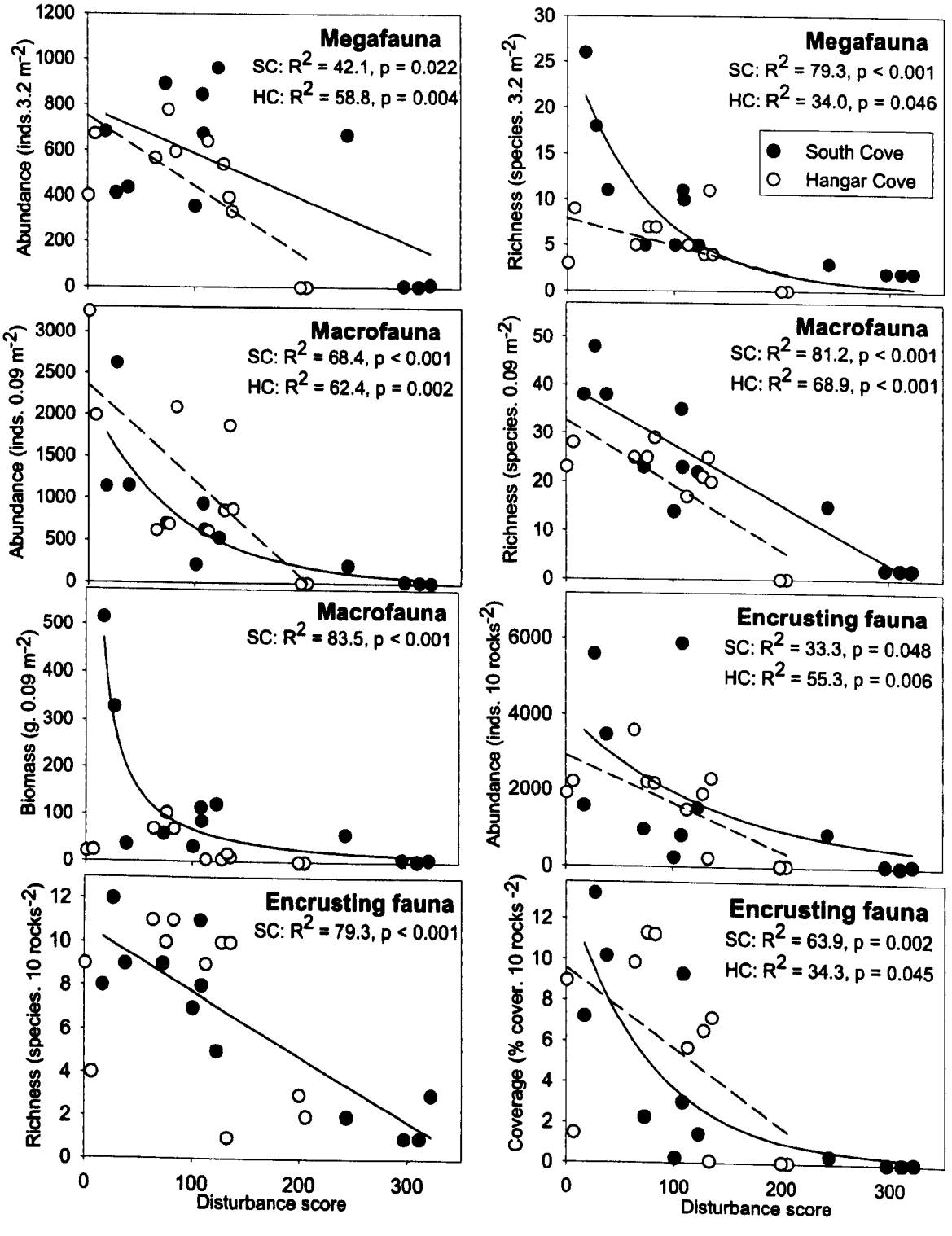

Figure 7.2 Plots of biological parameters against disturbance score (I_d) for each disturbance grid deployed at South Cove and Hangar Cove. Benthic assemblages were sampled at three resolutions to detect encrusting fauna, macrofauna and megafauna. The significant regressions through data from each site are shown (South Cove = solid lines, Hangar Cove = broken lines)

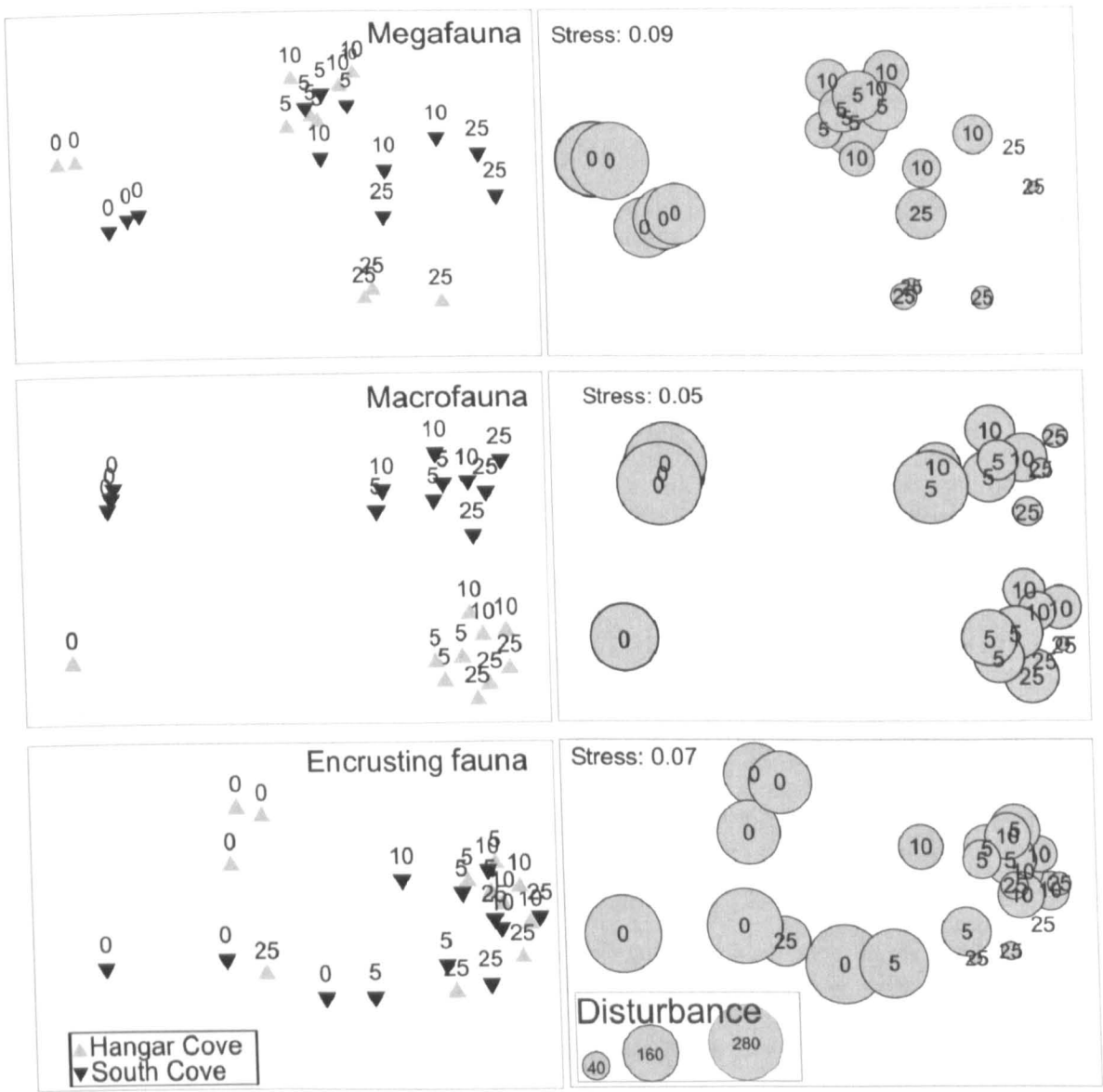

Figure 7.3 *Left:* MDS ordinations of abundance data collected from disturbance grids at each site (symbols) and depth (numerals). Bray-Curtis similarities were calculated from fourth-root transformed data. *Right:* Duplicate MDS ordinations with overlaying bubble plots to represent disturbance scores (plot areas = I_d) for each grid. Labels indicate the depth of each grid

Two-way ANOSIM tests showed that the three disturbance groups were statistically distinct, although the degree of dissimilarity between groups was moderate (Table 7.2). Furthermore, the BIOENV procedure indicated that disturbance intensity was the environmental variable that best grouped the disturbance grids in a manner consistent with the biological data. The megafauna samples from South Cove were best correlated with depth and disturbance, whilst all other sample sets from both sites were best correlated with disturbance as a single variable (Table 7.2). It is important to note that depth and disturbance were broadly correlated, and it is not possible to split the relative influence of these co-variables. Therefore, in effect only the depth/disturbance variable and the substrata parameter were tested in the BIOENV procedure, and ideally more environmental factors would have been quantified. Furthermore, a model matrix generated from the disturbance scores was correlated with the biological similarity matrices using the RELATE test. All sampling levels were significantly correlated with the model matrix, indicating a continuum of community change from low disturbance to high disturbance grids (Table 7.2). The strength of the correlations between each sampling level and the model matrix ranged from moderate (South Cove encrusting fauna, $\rho = 0.416$, $P = 0.007$) to high (Hangar Cove macrofauna, $\rho = 0.785$, $P = 0.001$). Interestingly, the correlations were generally greater at Hangar Cove than South Cove and the weakest correlations were found with the encrusting fauna samples at both sites.

Table 7.2. Results of multivariate tests applied to fourth-root transformed abundance data collected at each disturbance grid location. Two-way ANOSIM tests (site and disturbance) were used to assess the overall dissimilarity between disturbance groups (999 random permutations). The environmental variable(s) that best described the biological patterns were determined by using the BIOENV routine with continuous disturbance, depth and % cover of substratum data. The model matrix used for the RELATE test was generated from similarities in disturbance values (I_d) between samples. This matrix was then correlated with the biological similarity matrix for each sampling level.

ANOSIM (Global dist. groups)

Sampling level	**R**	**P**
Megafauna	0.424	0.001
Macrofauna	0.541	0.002
Encrusting fauna	0.457	0.002

BIOENV	**South Cove**		**Hangar Cove**	
Sampling level	**Best variable(s)**	**Corr.**	**Best variable(s)**	**Corr.**
Megafauna	Dist., depth	0.761	Disturbance	0.680
Macrofauna	Disturbance	0.809	Disturbance	0.662
Encrusting fauna	Disturbance	0.711	Disturbance	0.624

RELATE	South Cove		Hangar Cove	
Sampling level	ρ	P	ρ	P
Megafauna	0.695	0.001	0.733	0.001
Macrofauna	0.595	0.003	0.785	0.001
Encrusting fauna	0.416	0.007	0.634	0.003

SIMPER analysis determined which individual taxa contributed most to the observed dissimilarity between the disturbance groups (Table 7.3). It should first be noted that the overall dissimilarity between assemblages sampled at the moderate and highly disturbed grids was consistently much greater than the dissimilarity between the low and moderately disturbed grids. At all sampling levels the number of species and individuals sampled at the high disturbance grids (group 3) was considerably lower than at the low and moderate disturbance grids (groups 1 and 2). Hence, even after a fourth root transformation to down-weight abundant species, the taxa responsible for the dissimilarities between groups 2 and 3 were simply the most abundant taxa in the group 2 samples. At the megafauna sampling level, the highly abundant and motile limpet *Nacella concinna* and sea urchin *Sterechinus neumayeri* were high contributors to the dissimilarity between groups 2 and 3, whilst the differences in macrofauna were due largely to the bivalve *Mysella charcoti* and the polychaete *Leitoscoloplos kerguelensis* (all of which had greater abundances in the moderately disturbed samples compared with highly disturbed samples, see Table 7.3).

Interestingly, *Leitoscoloplos kerguelensis, Ophryotrocha* sp. and *Parborlasia corrugatus* are three species known to be associated with disturbed sediments (Barnes & Conlan 2007 and references therein) and had greater abundances at moderately disturbed grids compared with low disturbance grids (Table 7.3). Other key taxa responsible for the dissimilarities between groups 1 and 2 were the polychaete *Aphelochaeta* sp., the bivalve mollusc *Laternula elliptica*, the ophiuroid *Ophionotus victoriae* and unidentified nematodes, all of which had greater abundances in the low disturbance samples. Spirorbid polychaetes and the cheilostome bryozoan *Fenestrulina rugula* dominated encrusting assemblages at all grids and their numbers generally increased with decreasing disturbance frequency. As a result, these taxa were the principal contributors to the dissimilarities between all disturbance groups.

Table 7.3 The 5 taxa (at each sampling level) contributing most to the observed differences between disturbance groupings, as determined by the SIMPER routine (on fourth-root transformed data). Disturbance group 1 relates to the least disturbed grids, disturbance group 3 the most intensely disturbed. Overall dissimilarity between groups is shown in parentheses.

Dist. groups	Taxa	Av.Ab.	Av. Ab.	%	Cum %
Megafauna					
1 and 2	*Nacella concinna*	3.14	3.90	13.77	13.77
(45.47%)	*Ophionotus victoriae*	1.93	1.74	12.04	25.81
	Laternula elliptica	0.91	0.49	9.10	34.92
	Parbolasia corrugatus	0.00	0.48	5.13	40.04
	Sterechinus neumayeri	3.19	3.21	4.80	44.84
2 and 3	*Sterechinus neumayeri*	3.21	0.88	23.03	23.03
(71.52%)	*Nacella concinna*	3.90	2.21	21.66	44.69
	Ophionotus victoriae	1.74	0.00	12.32	57.01
	Odontaster validus	1.39	0.43	9.22	66.23
	Parbolasia corrugatus	0.48	0.00	4.85	71.08
Macrofauna					
1 and 2	*Aphelochaeta* sp.	2.10	1.14	3.67	3.67
(39.02%)	Nematodes	2.95	1.78	3.34	7.01
	Mysella charcoti	3.77	2.73	3.31	10.32
	Ophryotrocha sp.	1.08	1.68	2.84	13.15
	Leitoscoloplos kerguelensis	2.29	2.30	2.62	15.77
2 and 3	*Mysella charcoti*	2.73	0.65	5.65	5.65
(80.62%)	*Leitoscoloplos kerguelensis*	2.30	0.39	4.78	10.42
	Eatoniella calignosa	2.09	0.76	4.03	14.46
	Onoba turqueti	1.86	0.26	3.78	18.24
	Ophelina breviata	1.78	0.00	3.59	21.83
Encrusting fauna					
1 and 2	*Fenestrulina rugula*	4.37	2.92	14.48	14.48
(35.81%)	Spirorbid polychaetes	6.60	5.76	12.48	26.96
	Smittina rogickae	1.95	0.61	11.44	38.40
	Indet. cyclostome a.	1.19	1.65	8.32	46.72
	Micropora notialis	1.19	0.79	7.63	54.34
2 and 3	Spirorbid polychaetes	5.76	2.94	25.17	25.17
(62.13%)	*Fenestrulina rugula*	2.92	0.83	15.44	40.62
	Hippadanella inerma	1.45	0.45	9.60	50.22
	Indet. cyclostome a.	1.65	0.25	9.33	59.55
	Ellisina antarctica	1.31	0.00	9.29	68.84

The data also suggested a shift in life strategies with changing disturbance intensity, as the relative abundance of sessile fauna generally increased with decreasing disturbance (Fig. 7.4). Variation within each group was high, and differences between each group were non-significant. However, an overall linear regression of data from both sites showed a significant negative relationship between the disturbance intensity and the relative abundance of sessile fauna. This relationship was stronger at the macrofauna sampling level ($R^2 = 0.49$, $F = 21.08$, $P = 0.000$) compared with the megafauna level ($R^2 = 0.21$, $F = 5.52$, $P = 0.028$).

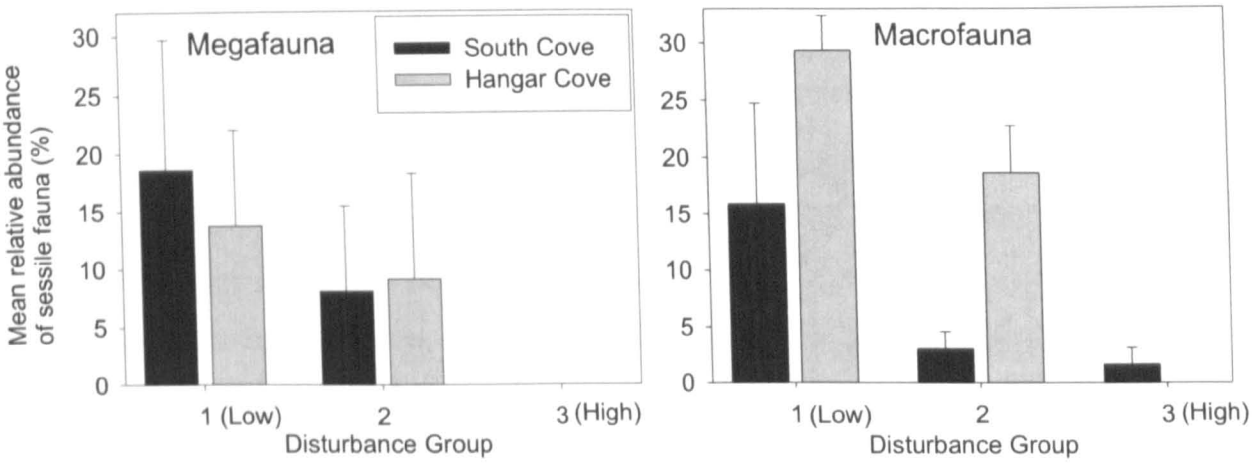

Figure 7.4 Relative abundance of sessile fauna for each disturbance group and site. Data are means of every grid within each disturbance group for each sampling level (± SE).

DISCUSSION

Disturbance intensity

Disturbance intensity was negatively correlated with almost all of the univariate measures of community structure and was the environmental variable most correlated with the multivariate abundance matrices. Ice disturbance, or more specifically scouring by icebergs and sea ice, is therefore a dominant environmental force acting on shallow water assemblages at Adelaide Island, and probably at similar polar coastal locations. Collisions between ice and benthos in shallow waters have been described as catastrophic (Conlan et al. 1998, Peck et al. 1999, Smale et al. in press) and, even if one considers the deeper waters of the continental shelf, iceberg scouring may be one of the five most significant natural disturbances acting on any ecosystem

(Gutt & Starmans 2001). The disturbance data presented in chapter 6 and linked with biological data in this chapter were measures of the frequency and force of iceberg impacts at each grid location. Unsurprisingly, within the range of disturbance intensities investigated in the current study, greater disturbance intensity was correlated with lower species richness, evenness, biomass, and space coverage. Communities were broadly distributed along a disturbance gradient and sessile fauna increased in relative abundance as disturbance intensity decreased.

What is counter-intuitive, however, is the significant decrease in total abundance with increasing disturbance recorded at all three sampling levels. Classically, highly disturbed areas are characterised by a low diversity of highly abundant pioneers (Pearson & Rosenberg 1978, Huston 1979, Sousa 1979). A continuous decrease in total abundance with increasing disturbance was recorded, although the strength of this relationship was moderate within the megafauna and cryptofauna sample sets. There are two possible explanations for this observation. Firstly, disturbance intensity was so great at the most disturbed grids (disturbance was recorded at some grids on almost every tri-monthly surveying occasion) that pioneer species were either absent or too small to be detected by the sampling method. Therefore, pioneers were abundant at the 'moderately' disturbed grids (there were a number of anomalies in abundance recorded at intermediate levels of disturbance) and abundance does decrease over a larger-scale disturbance gradient outside the range of this study. For example, typical pioneer species associated with disturbed habitats, such as the polychaetes *Leitoscoloplos kerguelensis* and *Ophryotrocha* sp. (both of which were entirely absent from the high disturbance areas) and spirorbid polychaetes, had greater abundances at the moderately disturbed grid locations than at the high disturbance areas and were major contributors to the differences between the two disturbance groupings. However, it is important to note that in addition to ice scouring frequency the carbon content of the sediment, which was not measured in the current study, may also influence the distribution of these deposit feeders (Conlan et al. 2004).

Secondly, the density of large sessile organisms increased as disturbance intensity decreased. At the low-intensity disturbance grids, the presence of large sponges, ascidians, erect bryozoans, terebellid polychaetes and large holothurians created a three-dimensional microhabitat ('multi-storied assemblages') with space for not only

more species, but also more individuals. For example, dense aggregations of the gastropod *Eatoniella calignosa*, the echinoid *Sterechinus neumayeri* and the holothurian *Cucumaria* sp. were observed in areas of low disturbance where sponges and ascidians were present. Large, structural species are an important component of Antarctic benthos (Gray 2001, Teixido et al. 2004) and are known to support a rich and abundant epifauna (Gutt & Schickan 1998, Gutt & Starmans 1998, Broyer et al. 2001). At the least disturbed locations in the current study sessile assemblages had sufficient time between disturbance events to develop (but disturbance was probably frequent enough to prevent mono-specific monopolisation) and created a more complex and spacious living space for an abundant epifauna.

The MDS ordinations of samples at all sampling resolutions suggested that communities at both sites were heterogeneous and patchy. Even at grids with low disturbance values, assemblages were dissimilar and not grouped closely together. Iceberg scouring is an inherently stochastic process and, like other disturbance pressures, promotes patchiness (Sousa 1984, Hall et al. 1992). Over larger spatial scales, patchy mosaics of disturbance events at different stages of recovery may actually increase habitat heterogeneity and niche separation, and therefore promote biodiversity (Gutt 2000, Gutt & Piepenburg 2003).

Also, the megafauna and macrofauna communities at 0 m depth (i.e. extreme low water spring tide level) were very poor in both richness and abundance, and as a result dissimilar to assemblages at other depths. This can be largely explained by the intense scouring by sea ice floes and brash at 0 m depth; on a number of occasions each of the 150 markers laid on the rocky shore were impacted by ice within 24 hours. However, in addition to frequent and intense ice scouring, wave action continuously turned over rocks during summer and the entire zone was covered by the ice foot during winter. In contrast, even in stormy conditions wave disturbance at >2 m depth is minimal at South Cove and Hangar Cove (personal observation), as they are largely sheltered from oceanic swells. Communities at 0 m depth were distinct from those at greater depths because of frequent turnover of semi-stable substrata (Sousa 1979), encapsulation by the ice foot (Barnes 1995b) and chronic ice scouring (Pugh & Davenport 1997), which resulted in the near denudation of surface life on the rocky shores of Adelaide Island (but see Waller et al. 2006).

Other environmental variables

Benthic assemblages were significantly different between the two study sites, which differed in a number of characteristics including exposure to disturbance and substratum type. The substratum at Hangar Cove was predominantly soft sediment, whilst South Cove was characterised by semi-stable hard substrata. It is likely that variation in community structure between locations was a result of differences in a number of localised conditions (Ragua-Gil et al. 2004), particularly exposure to disturbance and substratum type. Substratum type is a well-known factor influencing the distributions of benthic species at Antarctic locations (Gruzov et al. 1967, Kirkwood & Burton 1988, Barnes 1995c) and the distribution of major substratum types had a broad scale influence on the assemblages sampled at Adelaide Island.

The intensity of ice scouring in polar regions is broadly correlated with depth (Gutt & Starmans 2001, Laudien et al. 2007, Smale et al. 2007a), but small-scale deviations from the relationship may have an important role in the distribution of species in nearshore waters. Two of the disturbance grids considerably deviated from the depth-disturbance relationship: one of the 5 m depth grids at South Cove had a relatively low disturbance score and one of the 25 m depth grids at Hangar Cove had a comparatively high disturbance score. Small-scale differences in topography and substratum type were the most likely cause of these anomalies, although ice scouring frequency is highly variable over time (Smale et al. 2007a). The benthic assemblages at these grid locations were similar to those at grids with similar disturbance scores, rather than those at the same depths. To expand, the grid at South Cove at 5 m depth, protected by a small rise in topography and larger boulders, received fewer impacts than other grids at this depth and the assemblage here was more abundant, speciose and dominated by sessile forms; similar to assemblages at 10 m depth. Therefore, small-scale spatial variation in disturbance intensity (just 10s of metres) may allow relatively rich communities to develop in close proximity to frequently disturbed assemblages. It seems likely that the development of rich assemblages, acting as sources of potential recruits, may influence the recolonisation of fresh iceberg scours in nearby intensely disturbed areas (Peck et al. 1999, Conlan & Kvitek 2005).

Ecological models and future change

In the Arctic, studies on the effects of iceberg scouring in nearshore waters have described peaks in species richness where disturbance intensity is intermediate (Conlan & Kvitek 2005, Laudien et al. 2007), as could be predicted by the 'intermediate disturbance hypothesis' (Connell 1978, Huston 1979). In the current study, no intermediate peak in richness was recorded within the range of disturbance intensities examined. Icebergs or sea ice impacted almost all of the disturbance grids at least once during the two-year survey by Smale et al. (2007), suggesting that these sites are intensely disturbed, even at 25 m depth. Therefore, it is likely that the assemblages at these sites represent the 'disturbed end' of the disturbance gradient, and species richness may peak at intermediately disturbed locations outside the scope of this study (i.e. in deeper water or more protected sites).

It is currently unclear how climatic change will affect the intensity of ice disturbance acting on Antarctic benthic communities. It has been suggested that glacial retreat and increased iceberg loading into coastal waters will intensify disturbance pressure (Brown et al. 2004), but on the other hand warmer waters will reduce the life expectancy, and perhaps the population size, of travelling icebergs (see Wadhams 2000 for iceberg decay rates). Furthermore, a reduction in the duration of winter fast ice would increase the seasonal period of iceberg scouring (Chapter 6). There are, of course, many other uncertainties involved in predicting future disturbance rates. In the Weddell Sea system, a decreased frequency of disturbance events may be more detrimental to biodiversity than an increase (Johst et al. 2006). However, the data presented here suggest that any increase in the intensity of iceberg scouring would result in assemblages with fewer species, less individuals and lower biomass inhabiting the immediate subtidal zone at high latitudes.

Chapter 8 – General Discussion

Chapter 8 – General Discussion

MAIN CONCLUSIONS

The benthic communities at Rothera Point, Adelaide Island, were both rich and abundant despite being intensely disturbed by ice. Some disturbance grids deployed at the study sites were impacted by ice at least 6 times in 2 years (the mean number of hits for all 24 grids was 3.8 ± 1.7 per 2 years), indicating a high frequency of disturbance events in shallow waters. Despite this, ~170 different species were recorded from the five study sites and the maximum density of animals was in the order of 40,000 inds.m^{-2}. Richness was also high at the phylum level, with 15 phyla recorded in total. The research was carried out to answer the three main questions stated in Chapter 1, and the results can be summarised as follows:

1) Is there any evidence of community change along environmental gradients in the study region?

Benthic assemblages change significantly along a bathymetric gradient in the shallows at Adelaide Island, and probably generally in polar habitats (Chapter 3). Species and phylum richness, the abundance of sessile forms and the homogeneity of the benthos all increase with depth from 0 to 35 m depth. However, assemblages changed continuously along the environmental gradient and did not form distinct depth bandings or zones. Depth-related distributions of assemblages have been reported from other Antarctic locations and ice disturbance has been frequently proposed as the physical force driving the biological patterns. However, the data presented in Chapter 6 shows, for the first time, that the intensity of ice-mediated disturbance is inversely related to depth. This strongly suggests that benthic assemblages are distributed along a disturbance gradient in nearshore polar waters. Furthermore, it seems likely that the significant differences in community structure between sites just a few kilometres apart are largely due to variation in exposure to ice disturbance, although this requires further investigation.

2) If ice disturbance is a driving force influencing patterns of community structure, what are the direct effects of a disturbance event?

Assemblages in recently formed iceberg scours have significantly lower richness, abundance and biomass values compared with assemblages in relatively undisturbed areas (Chapter 4). The sampling suggested that iceberg disturbance events are catastrophic at small spatial scales regardless of site-specific differences in granulometry and background community. In terms of post-disturbance recovery, even simple communities comprising of a small number of species may require ~10 years to recover to pre-perturbed levels of abundance and diversity (Chapter 5). However, if size and age characteristics of recovering assemblages are also considered, decades or centuries may be required for complete recovery due to slow recruitment and growth rates in the Antarctic. Extreme variability in recovery rates was observed between iceberg scours, whilst 'undisturbed' reference communities at the highly disturbed study site were highly patchy. It seems that ice disturbance promotes both habitat heterogeneity and assemblage patchiness at small spatial scales (i.e. 10s of metres) at Adelaide Island.

3) Does the intensity of ice disturbance determine community structure?

The intensity of iceberg disturbance at Adelaide Island demonstrated clear patterns with both season and depth, and was significantly different between sites and years (Chapter 6). The depth-related patterns were perhaps due to iceberg size frequencies, whilst differences between seasons, sites and years could be explained largely by the presence or absence of fast sea-ice. Within each study site, community parameters such as richness, abundance, biomass, areal coverage and multivariate community structure were correlated with disturbance intensity (Chapter 7). However, communities were significantly different between study sites, and it is likely that factors other than disturbance, such as substratum type and oceanographic currents, influence benthic community structure at larger spatial scales. In addition to ice scouring, the rocky shore habitat (0 m depth) was disturbed by the winter ice foot, wave action and emersion periods. As a result, rocky shore communities were depauperate in numbers of both species and individuals, and were highly distinct from those in the subtidal zone.

ECOLOGICAL IMPLICATIONS OF CURRENT FINDINGS

Disturbance in the context of other community-structuring factors

There is considerable evidence presented within this thesis to suggest that the intensity of ice-mediated disturbance is a major structuring force acting on benthic communities in the shallows of Adelaide Island. The shallow subtidal zone, from the intertidal rocky shore down to 40 m depth, represents a steep environmental gradient driven largely by ice disturbance. Similar to other habitats characterised by strong environmental gradients, such as mountain slopes or temperate rocky shores, it seems that communities in polar nearshore habitats are broadly (but patchily) distributed along the dominating physical gradient. However, marine communities are extremely complex, and many factors govern the distribution of species and assemblages (Underwood 1980, White & Pickett 1985, Menge et al. 1997, Underwood 2000). It is therefore important to consider the influence of ice disturbance on community structure within a wider context of biological and physical factors.

Studies conducted at other Antarctic locations have also suggested that ice disturbance, in the form of anchor ice (Dayton et al. 1974), the ice foot (Barnes 1995b, Waller et al. 2006) and iceberg scouring (Zamorano 1983, Sahade et al. 1998, Brown et al. 2004) is the most influential factor driving patterns in community structure. However, wave disturbance (Westermeier et al. 1992), sediment slumping (Slattery & Bockus 1997), substratum profile and type (Kirkwood & Burton 1988, Barnes 1995c, Sahade et al. 1998), current flow (Ragua-Gil et al. 2004), light input (Gambi et al. 1994), depth (Nonato et al. 2000), salinity and fast ice cover (Barnes 1995c) have all been suggested as important community-structuring physical factors. In addition, anthropogenic pressures such as oil spills (Smith & Simpson 1998) and pollution (Lenihan & Oliver 1995) may alter community structure in Antarctic nearshore environments.

At Adelaide Island, an analysis of the relative influence of depth, disturbance and broad-scale substratum type (Chapter 7) showed that disturbance was most related to the observed changes in community structure. However, each study site at Adelaide Island supported highly distinct benthic communities. It seems that these differences

in community structure can be largely explained by variation in substratum type, slope and current flow between sites. On a larger spatial scale, Ragua-Gil et al. (2004) also found that differences in localised environmental conditions, rather than geographical distance, were the most likely cause of between-site variation in benthic communities. Furthermore, as the study sites were on the sheltered eastern coastline of Adelaide Island they were not exposed to intense wave action, which is likely to be much more significant at other sites on the island. A combination of high wave energy and dense floating ice would undoubtedly create extremely disturbed conditions and result in a very different community. Other factors such as anthropogenic disturbance, salinity and light regimes are almost certainly less influential at Adelaide Island, as they are either negligible, very localised or fairly consistent between sites. In the context of physical factors that structure the benthos over ecological timescales, it seems that at Adelaide Island (and probably around most of coastal Antarctica) ice disturbance is of primary importance. The data presented in this thesis supports the work by Gutt and Starmans (2001), which suggested that ice disturbance is amongst the five most significant natural disturbances acting on any ecosystem and, as a result, most Antarctic shelf communities never reach peak maturity.

Community development in the Antarctic, as elsewhere, is also influenced by a suite of biological factors. There are currently considerably fewer studies on processes such as predation, competition, recruitment and mutualism from polar regions compared with lower latitudes. However in the last 20 years significant advances have been made in areas including larval ecology, settlement, competition for space and predator-prey relationships at high latitudes. In a comprehensive 3-year study using artificial panels at Adelaide Island, Bowden et al. (2006) suggested that post-settlement disturbances predominantly control community development. They suggested that whilst ice disturbance was influential, intense grazing by macrobenthos was more important and resulted in widespread paucity of colonisation on the upper surfaces of the panels, which were exposed to dense feeding aggregations of molluscs and echinoids. Furthermore, other biological disturbances, such as tube-building by terebellid worms, significantly affect assemblage development at Adelaide Island (Bowden et al. 2006). It is evident that whilst the general patterns of community structure reported in this thesis are largely due to the physical gradient of ice

disturbance, biological disturbances at various temporal and spatial scales also strongly influence benthic development and structure.

Other biological factors that are likely to have affected benthic community structure at Adelaide Island include episodic recruitment events, the input of phytoplankton and the frequency of scavenging opportunities. At lower latitudes, it has been shown that variation in oceanic conditions can create variability in populations at the bottom of the food chain, which subsequently cascade up the trophic system and affect populations of top consumers (so called 'bottom-up' effects, see Menge et al. 1997, Menge 2000, Witman et al. 2003). Recruitment in the Antarctic appears to be seasonal, but does vary between taxa and years (Stanwell-Smith & Barnes 1997, Bowden 2005b). It seems that intense episodic recruitment events, caused by changes in oceanic conditions, could have significant and wide-ranging effects on benthic community structure.

Dayton and Oliver (1977) sampled two areas at McMurdo Sound, one eutrophic and the other oligotrophic, and found entirely distinct communities. The benthos influenced by plankton-poor water originating from beneath the Ross Ice Shelf was considerably lower in abundance and diversity than the benthos that received an intense, seasonal input of plankton from open ocean currents. There are no large ice shelves around Rothera Point, but small-scale variation in the amount of phytoplankton reaching the seafloor may directly influence benthic assemblages, particularly in terms of the densities and forms of primary consumers.

Finally, the nearshore waters around Antarctica support a high diversity and abundance of scavengers, which may contribute significantly to benthic composition (Richardson & Hedgepeth 1977, Presler 1986, Zamorano et al. 1986, Arntz et al. 1994). At Adelaide Island, Smale et al. (2007b) observed significant differences in scavenging behaviour between Hangar Cove and South Cove and between summer and winter. The likelihood of scavenging opportunities occurring at any particular area of seabed is, to some degree, linked to the frequency of ice scouring as catastrophic disturbances cause high mortality and damage to benthos (Peck et al. 1999, Conlan & Kvitek 2005). However, periodic food falls such as vertebrate carcasses and faeces also attract scavengers and may alter community structure for

some time (Collins et al. 1999, Yau et al. 2002). For example, the benthic assemblages inhabiting the shallows near penguin colonies or seal breeding beaches may be primarily influenced by organic enrichment and increased scavenging opportunities rather than physical disturbance.

To summarise, the nearshore benthic communities around Rothera Point are strongly influenced by ice disturbance, which is perhaps the principal structuring force at this location. In this context, ice disturbance is comparable to other disturbance pressures, which also play a major role in structuring communities in very different habitats, both in the marine and the terrestrial realm. For example, the composition, age and functionality of assemblages in estuaries are also largely structured by the intensity of, and interval period between, disturbance events. In these habitats, extreme fresh water inflow events alter the physio-chemical environment, which in turn considerably influences benthic community structure (Mannino & Montagna 1997, Kimmerer 2002). Similarly, plant and animal communities inhabiting coastal wetlands are strongly influenced by seasonal flooding, which is perhaps the principal force determining community structure (Odum et al. 1995). Other key disturbances structuring natural communities include the frequency of storms influencing coral reefs (Connell 1997) and the intensity of fishing in certain soft-bottom habitats (Kaiser et al. 2000). It is important to note that, as with ice disturbance, some other disturbance pressures may promote biodiversity at larger spatial scales by creating patchy mosaics of disturbance events at differing stages of recovery. Perhaps the most obvious example of this phenomenon is forest fires, which have been shown to promote biodiversity over certain temporal and spatial scales (Vanderwoude et al. 1997, Moretti et al. 2004).

Ice disturbance and climate change

It is now known that the West Antarctica Peninsula region has warmed rapidly in the past half century, in terms of both air temperature (King & Harangozo 1998, Vaughan et al. 2003) and surface ocean temperature (Meredith & King 2005). Predicting and detecting the effects of this warming is complicated and has resulted in considerable uncertainty and debate (Clarke et al. 2007). However, there is evidence to suggest that the extent and duration of winter fast ice is decreasing in some regions (Murphy et al.

1995, de la Mare 1997) including the West Antarctic Peninsula (Smith & Stammerjohn 2001). It is also evident that many glaciers, such as the Sheldon Glacier on Adelaide Island, are retreating rapidly (Cook et al. 2005). What is not clear, however, is whether the number of icebergs in the Southern Ocean is increasing. On one hand, satellite images have been used to show that the number of Antarctic icebergs is rising (Bindschadler & Rignot 2001), whilst other researchers suggest that the reported rise may simply be a relic of improved observation tools (Long et al. 2002). Furthermore, the number of very large icebergs observed calving from ice sheets has risen, such as the largest iceberg ever recorded ('B15') which broke off from the Ross Ice Shelf in 2000.

If glaciers continue to retreat and more ice shelves disintegrate, it seems likely that the number of floating icebergs will increase, which in turn would potentially increase the frequency of iceberg impacts with shallow water benthos. Furthermore, icebergs will be 'locked-in' for fewer months of the year if the duration of winter fast ice decreases, perhaps resulting in more disturbance events through the year. The data collected at Adelaide Island unequivocally shows that; iceberg impacts are catastrophic to benthic communities; assemblages are broadly distributed along a disturbance gradient; high disturbance intensity correlates with low assemblage richness, biomass and abundance. Thus, an increased disturbance intensity at the regional scale would have wide-ranging effects on benthic communities, with bathymetric or latitudinal shifts in species distributions a likely consequence.

Directions for further research

The research was largely successful in that it addressed the broad questions set out in the introduction. The work has comprehensively shown iceberg impacts to be catastrophic to benthic assemblages and has highlighted the considerable variability in the rates of post-disturbance recovery. Furthermore, it demonstrated, for the first time, that the intensity of ice disturbance varies with depth, site, season and year and that this variability strongly influences benthic community structure. However, there are two fundamental areas of polar marine ecology which require more attention, both of which were highlighted by the current research.

1) The first main area relates to the physical agents of disturbance. Currently, very little is known of the distributions, size frequencies, formation processes and degradation rates of icebergs in the Southern Ocean. Orheim (1985) estimated that the total population of Antarctic icebergs (>10 m wide) was >300,000 in 1981-1984, but there are no comparable studies in the recent literature. It is therefore difficult to predict how environmental change will affect the frequency of iceberg-mediated disturbance intensity in Antarctic waters. However, recent advancements in satellite technology have facilitated iceberg tracking and provided new insights into iceberg formation (e.g. Gladstone & Bigg 2002, Rack & Rott 2004, Schodlok et al. 2005). Such technologies could be applied to monitor changes in the number, sizes and degradation rates of icebergs in the Southern Ocean, which is fundamental for testing the hypothesis that the frequency of iceberg scouring will increase during periods of glacial retreat and iceberg loading.

The rapid warming of the Antarctic Peninsula over the last 50 years (King & Harangozo 1998, Vaughan et al. 2003) is likely to have wide-ranging consequences. Long-term monitoring to detect changes in the environmental parameters that structure shallow water benthos (e.g. sedimentation rates, fresh water input, fast ice duration, extent of winter ice foot) should be a priority. Furthermore, observations of shallow water benthic community structure over decadal timescales are increasingly important. Long-term studies on benthic community change have been conducted at lower latitudes (e.g. Coull 1985, Connell 1997, Kollmann & Stachowitsch 2001) and could easily be carried out at the many permanent research stations throughout Antarctica.

2) Compared with temperate and tropical marine ecology there is currently a distinct paucity of field manipulation studies in polar regions. For example, three recent British Antarctic Survey PhD dissertations conducted at Rothera Point (Brockington 2001, Bowden 2005, and the current work) have suggested that intense grazing by *Nacella concinna* and *Sterechinus neumayeri* is a key structuring force acting on community development in the shallow subtidal zone. Despite this, there have been no experimental field manipulations of grazer densities in the Antarctic, even though such studies are common in the temperate marine ecology literature (e.g. Commito & Shrader 1985, Andrew & Underwood 1993, Menge et al. 1997, Korpinen et al. 2005).

Without field manipulations of grazer, predator and competitor densities, it is not possible to quantify the importance of these biological processes in structuring benthic communities. Similarly, the temperate literature has highlighted the importance of studying processes at large spatial scales (i.e. regional), rather than focusing purely on site effects (Menge 2000, Witman et al. 2003). Although this is logistically much more challenging in Antarctica, recent studies such as the regional biodiversity assessment conducted by (Brandt et al. 2007) suggest that sampling at large spatial scales is a possibility.

Finally, this thesis has demonstrated that recovery rates of benthic communities following iceberg impacts are highly variable, even when considering simple assemblages distributed across small spatial scales. If the frequency or intensity of disturbance events is changing along the Antarctic Peninsula, it is crucial to increase our understandings of post-disturbance recovery processes. The study presented in Chapter 5 monitored just three iceberg scours for the first 32 months of recovery and yet it is the most comprehensive study of its kind in Antarctica. In contrast, disturbance and recovery patterns in coral reef communities have been studied for 30 years (Connell et al. 1997), whilst recovery from mechanical cockle-dredging has been monitored for 10 years (Piersma et al. 2001) and benthic recovery following an oil spill has been studied for 13 years (Smith & Simpson 1998). There are many more examples of long-term monitoring following disturbances in tropical and temperate regions, and the paucity of similar studies at high latitudes can perhaps be explained by the relative recency of permanent year-round field stations and logistical difficulties. Nonetheless, there is an apparent need for longer-term field studies on the effects of ice disturbance, especially if the frequency of such disturbances is likely to be affected by climate warming.

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Appendix – List of taxa

Appendix 1. Full list of taxa sampled at South Cove and Hangar Cove, Adelaide Island, Antarctica during sampling for Chapter 7. The sampling level(s) (1 = megafauna, 2 = macrofauna and 3 = encrusting fauna) and disturbance group(s) (1 = low disturbance, 3 = high disturbance) taxa were recorded in are also shown.

TAXA		OCCURRENCE	
Class	**Family/ Genus- Species**	**Sample**	**Dist. group**
Demospongiae	*Dendrilla antarctica*	1	1
	Sphaerotylus antarcticus	1	1
	Mycale acerata	1, 2	1, 2
	Bubaris antarctica	2	1
Anthozoa	*Edwarsia* sp.	1	1, 2
	Isotaelia antarctica	1	1, 2
	Hormathia sp.	1	1
	Indet Actiniidae (burrowing)	2	1, 2, 3
Hydrozoa	Indet. hydroids (bush form)	1, 2	1
Anopla	*Parborlasia corrugatus*	1	1, 2
	Antarctonemertes validum	1, 2	1, 2, 3
Priapulidea	*Priapulus tuberculatospinosus*	2	1, 2
Sipunculidea	*Golfingia* sp.	2	1
Turbellaria	Indet. Turbellarian	2	1, 2
Adenophorea	Indet. nematodes	2	1, 2
Polychaeta	*Barrukia cristata*	1, 2	1, 2, 3
	Aglaophamus antarctica	2	1, 2, 3
	Lumbrineris cingulata	2	1, 2
	Steggoa magalhaensis	2	1, 2, 3
	Nematonereis sp.	2	1, 2
	Leitoscoloplos kerguelensis	2	1, 2,3
	Capitella sp.	2	1, 2, 3
	Ophryotrocha sp.	2	1, 2, 3
	Rhodine intermedia	2	1
	Ophelina breviata	2	1, 2, 3
	Apistobranchus gudrunae	2	1, 2, 3
	Myrianida cf. *proceraeae*	2	1, 2
	Autolytus charcoti	2	1, 2
	Spiophanes tcherniai	2	1
	Thelepus cincinnatus	1, 2	1, 2
	Pyllodoce patagonica	2	1
	Aphelochaeta sp	2	1, 2, 3
	Kefersteinia fauveli	2	1, 2
	Typosyllis armillaris	2	1, 2
	Neanthes kerguelensis	2	1, 2
	Flabelligera mundata	1	1, 2
	Indet. Spirorbidae	3	1, 2, 3
	Indet. Serpulidae	3	1, 2
Gastropoda	*Nacella concinna*	1, 2	1, 2, 3
	Margarella antarctica	1, 2	1, 2, 3
	Iothia coppingeri	1, 2	1, 2
	Eatoniella calignosa	2	1, 2, 3
	Onoba turqueti	2	1, 2, 3
	Onoba gelida	2	1, 2, 3

	Onoba kergueleni	2	1
	Toledonia limnaeformis	2	1, 2
	Toledonia punctata	2	1, 2
	Laevilitorina antarctica	2	1, 2, 3
	Marseniopsis mollis	1	1
	Tritionella belli	1	1
	Notaeolidia depressa	1, 2	1, 2, 3
	Austrodoris kerguelensis	1	1
Polyplacophora	*Callochiton steinii*	2	1, 2
Bivalva	*Adacnarca nitens*	2	1, 2
	Mysella charcoti	2	1, 2, 3
	Yoldia eightsi	1, 2	1
	Cyamiomactra laminifera	2	1, 2
	Thyasira bongraini	2	1
	Laternula elliptica	1, 2	1, 2, 3
	Philobrya sublaeris	2	1, 2
	Philobrya wandelensis	2	1, 2
Malacostraca	*Campylaspis maculata*	2	1, 2, 3
	Vaunthompsonia inermis	2	1, 2
	Eudorella fallax	2	1, 2, 3
	Caecognathia antarctica	2	1, 2
	Harrietonana cf subtriangulata	2	1, 2, 3
	Cymodoce antarctica	2	1, 2, 3
	Austrosignum glaciale	2	1, 2, 3
	Austofilius serratus	2	1, 2
	Munna sp.	2	1, 2
	Paraceradocus gibber	2	1, 2
	Schraderia gracilis	2	1, 2, 3
	Methalimedon nordenskjoeldi	2	1, 2, 3
	Oradarea rossi	2	1, 2
	Oradarea tridentate	2	1, 2
	Oradarea edentata	2	1, 2, 3
	Thaumatelson herdmani	2	1, 2, 3
	Pachychelium nichollsi	2	1, 2
	Antatelson walkeri	2	1, 2
	Indet. Phoxocephalidae	2	1, 2
	Cheirimedon femoratus	2	1, 2, 3
	Prostebbingia brevicornis	2	1, 2, 3
	Prostebbingia longicornis	2	1, 2, 3
	Indet. Calliopiidae	2	1, 2
	Monoculodes cf *scabriculosus*	2	1, 2, 3
	Indet. Oedicerotidae	2	1, 2, 3
	Gondogeneia antarctica	2	2
	Nototanais dimorphus	2	1, 2, 3
	Indet. Philomedidae	2	1, 2, 3
	Hemicythere sp.	2	1, 2, 3
	Philomedes sp. b	2	1, 2, 3
	Scleroconcha sp.	2	1, 2, 3
Pycnogona	*Pentanymphon antarcticum*	2	1
	Austrodecus sp.	2	1, 2
	Nymphon sp.	2	1
	Austropallene sp.	2	1
Echinoidea	*Sterechinus neumayeri*	1, 2	1, 2, 3
Ophiuroidea	*Ophionotus victoriae*	1, 2	1, 2, 3
Asteroidea	*Odontaster validus*	1, 2	1, 2, 3
	Cryptasterias turqueti	1, 2	1, 2
	Diplasterias brucei	1, 2	1, 2
	Perknaster aurorae	1	1
	Porania antarctica	1	1
Holothuroidea	*Heterocucumis steineni*	1, 2	1, 2

	Cucumaria sp	1, 2	1, 2
	Echinopsis acanthocola	1, 2	1
Crinoidea	*Promachocrinus kerguelenses*	1	1
Ascidacea	*Cnemidocarpa verrucosa*	1, 2	1, 2
	Pyura discoveri	1	1
	Sycozoa sigillinoides	2	1
	Indet. Dideminidae	1	1
Stenolaemata	*Tubulipora* sp.	3	1, 2, 3
	Discoporella sp.	3	1
Gymnolaemata	*Kymella polaris*	1	1
	Aimulosia antarctica	3	1
	Arachnopusia inchoate	3	1, 2, 3
	Beania erecta	3	1
	Cellaporella antarctica	3	1, 2, 3
	Cellaporella bougainvillea	3	1, 2, 3
	Ellisina antarctica	3	1, 2
	Fenestrulina rugula	3	1, 2, 3
	Hippadanella inerma	3	1, 2, 3
	Micropora notialis	3	1, 2
	Smittina rogickae	3	1, 2
	Valdemunitella lata	3	1
	Xylochotridens rangifer	3	1, 2, 3